Taphonomic biases on the preservation of within-community seed size distributions

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April 30, 2003

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ABSTRACT

Seed size distributions from the fossil record have been used by paleobotanists for paleoclimatological and paleoecological interpretation and reconstruction. However, the fidelity of the seed size distribution of a fossil assemblage to that of its source community had not been tested. Taphonomic filters such as transport, predation, biodegradation, abundance, and sampling issues may selectively preserve or destroy seeds on the basis of size, thus causing the seed size distribution of a fossil assemblage to differ from that of the living community represented by this assemblage. The study presented here is a live-dead study in which I have compared the seed size distributions of a potential fossil assemblage and the living plant community that it represents. The potential fossil (or "death") assemblage consists of 44 seed taxa/morphotypes extracted from sediment cores collected in a tidal estuary, and the life assemblage consists of 41 seed plant species currently living in the water and on the hillside adjacent to the location of the sediment cores.

The results of this study show no statistically significant difference between the seed size distributions of the life and death assemblages. Although similar tests remain to be conducted in different depositional settings, it appears that taphonomic filters affecting seed size distributions are not strong and that the use of seed size distributions from fossil assemblages in paleoecological and paleoclimatological interpretation and reconstruction is not without merit.

INTRODUCTION

The fossil record is far from complete. Only a very small fraction of all the organisms that have ever lived have been preserved or will be preserved as fossils. Moreover, the fossil record is strongly biased, so that organisms which are large, abundant, contain mineralized parts, and/or live in depositional environments are much more likely to be preserved than those that are small, uncommon, soft-bodied, and/or live in erosional environments. These and other biases act at all scales from global to local, and make it difficult for paleontologists to accurately reconstruct ancient communities and ecosystems from fossil assemblages (Behrensmeyer et al., 1992; Donovan and Paul, 1998).

Taphonomy is the study of burial and fossilization. An understanding of the processes by which organisms are preserved can greatly assist in the reconstruction of paleocommunities and the interpretation of changes in the structure of ecosystems over geologic time. A common approach to examining taphonomic problems is the live-dead study (Kidwell, 2001). In this type of study, presence/absence, abundance, size, or other types of data are collected for an organism or group of organisms living in a particular area. The same types of data are then collected for the dead organisms in that area or, ideally, buried in the sediment directly beneath it. These represent the potential fossil assemblage of that community. The life assemblage and death assemblage are then compared by using any of a variety of statistical methods, in order to quantitatively assess the fidelity of the death assemblage to the life assemblage (Behrensmeyer et al., 2000; Greenwood, 1991; Spicer, 1990).

The proposed project is a live-dead study in which I will examine the taphonomic filters affecting the preservation of seed size distributions in a tidal estuarine setting.

SEED SIZE IN MODERN PLANTS

Living plants produce seeds that display a great variety of forms, and which range in size over 10 orders of magnitude (Harper et al., 1970). Seed size varies not just between species, but also within species, and even individual plants may produce mature seeds of differing size (Collinson, 1993). The size of seeds is influenced by a number of interrelated factors, discussed below.

1. Reproductive Strategy –

Due to energetic constraints, there is a tradeoff between number of seeds and size of seeds, so that a plant can produce a large number of small seeds, a small number of large seeds, or an intermediate number of mid-sized seeds (Shipley and Dion, 1992). Larger seeds provide more nutrients to the seedling, allowing it to develop larger leaves and roots before it becomes self-sufficient. Thus, selective forces external to the parent plant will influence which reproductive strategy will optimize the chances of a seedling's survival. These external selective forces include effects of local environment and climate. Larger seeds increase the chances of a seedling's survival in conditions of shade, drought, and competition for light, water and nutrients with other seedlings (Haig and Westoby, 1989). Smaller seeds are generally found in plants that grow in open, well-lit habitats (Tiffney, 1986). Lord et al. (1997) showed that tropical floras have larger seeds than temperate floras, regardless of dispersal mode and growth form.

2. Growth Form and Size of the Adult Plant –

Small adult plants are unable to produce very large seeds (Thompson and Rabinowitz, 1989). Consequently, the growth form of a plant can affect the size of the seeds it can produce. For instance, trees generally have larger seeds than shrubs, which generally have larger seeds than herbs, of which perennials tend to have larger seeds than annuals (Westoby et al., 1992).

3. Dispersal Mode –

Seeds are dispersed through a wide variety of means, both biotic (by sticking to the skin, fur or feathers of animals, or by being ingested and subsequently deposited in the feces of animals) and abiotic (transport by wind or water, or by actively "tossing" seeds from exploding fruits). Seeds dispersed by each of these methods can vary greatly in size, but in general the largest seeds are biotically dispersed and the smallest are abiotically dispersed (Tiffney, 1986).

SEEDS AND SEED SIZE IN THE FOSSIL RECORD

Seeds are not at all uncommon in the fossil record. The oldest known seeds are Famennian in age (Gillespie, Rothwell, and Sheckler, 1981), and were very small (Tiffney, 1986). Since their appearance, seeds have evolved a great diversity of sizes and forms. Seeds are sometimes found associated with other plant organs, such as leaves, wood, roots, flowers and pollen. Often, however, fossils beds are found which consist primarily of seeds, and little of anything else. These types of assemblages may be due to quicker rates of biodegradation for leaves than for seeds, or by the simultaneous deposition of floating pockets of seeds during a drop in water level (Collinson, 1983b). Seeds are known from virtually all kinds of depositional environments, including lacustrine, fluvial, near-shore marine and tidal estuarine deposits (Plint, 1983, 1988).

Because seed size correlates with the factors discussed above, the distributions of seed sizes from fossil assemblages have been used in paleoecological and paleoclimatological reconstructions. Also, changes in seed size distributions over geologic time have been interpreted as representing changes in climate and ecosystem structure (Tiffney, 1986; Wing and Boucher, 1998; Eriksson et al., 2000). These studies make several assumptions, including the assumption that the fossil assemblages accurately represent their source communities and are not biased by any taphonomic filters. However, taphonomic biases affecting seeds and seed size distributions may greatly influence the reliability of their application to these problems (Collinson, 1983b).

POTENTIAL TAPHONOMIC FILTERS

1. Transport by Wind or Water –

Many seeds (both modern and fossil) show specializations for wind dispersal, notably small size, wings, or hairs. Modern water dispersed seeds show a range of sizes from very small to the largest seeds in the world today, the double-coconut (*Lodoicea seychellarum*) (Westoby et al., 1992). The smaller forms may be disc-shaped with or without hairs along the periphery, allowing them to utilize the surface tension of water. This particular morphology is only effective in relatively quiet water. The larger forms, as in the double-coconut, rely on hollow chambers or light, spongy tissue. As these are buoyant and are not merely resting on the water's surface, they are much less affected by agitation of the water (Burnham, 1990). Fossil seeds have been described which display all of these characters (Tiffney, 1986).

Seeds can be transported vast distances from their source communities by wind and especially by water, sometimes >1000 miles (Ridley, 1930). Drifted and wind-borne seeds thus pose a significant problem to the reconstruction of fossil floras (Collinson, 1983b). Burnham (1990) studied a mangrove island in which the drifted seeds and fruits were almost entirely from species not found living on the island. In addition to carrying seeds away from their source communities, transport by water may sort seeds according to their hydrodynamic properties or by their size (Collinson, 1993).

2. Diagenesis and Selective Biodegradation –

Compression of sediments containing seeds can alter their shape and size. In addition, the mode of preservation of seeds can affect their resistance to compression,

erosion once they are exposed, and to damage during collection (Collinson, 1993). Even before these take place, seeds which have comparatively thin walls may be more prone to biodegradation than those with thick walls, especially in oxidizing environments (Collinson, 1983b).

3. Predation –

Seeds may be partially or entirely consumed by a variety of vertebrates and invertebrates. They may be eaten directly off of the parent plant, while on the ground, or even after shallow burial in sediment. Different seed-eating animals may prefer to consume particular species, or seeds within a particular size range. Additionally, if seeds are abundant, an animal may preferentially consume seeds that are towards the larger end of its preferred size range. Thus, depending on the type of seed-eating animals present, as well as local environmental conditions, seeds may be selectively consumed on the basis of size. (Westoby et al., 1992)

4. Abundance –

By virtue of sheer numbers, more abundant seeds will have a greater probability of being buried and fossilized. Smaller seeds are likely to be produced in greater numbers than larger seeds, given parent plants of roughly the same size. However, a tree may be able to produce a comparable number of large seeds to the number of small seeds an herb can produce. The relative abundance of large versus small seeds in a community will therefore be related to the abundances of species with different growth forms and seed dispersal modes in that community. (Westoby et al., 1992; Behrensmeyer et al., 2000)

5. Sampling Issues –

The number of species found in a potential fossil assemblage can vary greatly depending on the sampling methods used, for instance, quadrat vs. transect sampling (Burnham, 1990). Additionally, some sampling methods may be biased towards small or large seeds. Sampling by sight, for instance, will most likely favor the collection and identification of larger seeds (Collinson, 1983a). It is also important to take into account the geographical location of samples. Most fossil seed assemblages are known from the Northern Hemisphere, particularly Europe and to a lesser extent North America (Eriksson et al., 2000). Because of the effects of climate and latitude on seed size (mentioned above), the seed size distributions of these assemblages may not accurately reflect the global condition at the time they were deposited. There may also be some error due to the inclusion of immature seeds in analyses, and these may be difficult to recognize in the fossil record (Tiffney, 1986).

PREVIOUS WORK AND SETTING OF STUDY

A considerable number of taphonomic studies of plant communities have been performed, but these have mostly utilized leaves or pollen, and ignored seeds. Live-dead

studies that do include seeds (Collinson, 1983b, 1993; Burnham, 1990) have not attempted to relate the seed size distributions of death assemblages to their source communities. Furthermore, none of these studies have been performed in tidal estuarine environments. I conducted the project presented here in just such a setting.

OBJECTIVES

In this study I explored the following questions which are pertinent to paleobiological research:

1. How well does the seed size distribution of a fossil assemblage reflect the seed size distribution of the flora that produced it?
2. What are the most important taphonomic filters affecting the preservation of seeds?
3. Which of these filters will preferentially preserve or destroy seeds of certain sizes?

I addressed these questions by extracting seeds from sediment cores collected in an active depositional site and quantitatively comparing the seed size distributions of these seeds (the death assemblage) and the local flora (the life assemblage). In order to assess the impact of particular taphonomic biases, I compared different combinations of subsets of both assemblages, defined on the basis of dispersal mode, growth form, and location at the site. I have also examined the grain size distributions of four of the sediment cores in order to determine whether sorting by transport in water has occurred. If there is a strong correlation between seed- and grain size among the samples, this would be consistent with sorting of the seeds according to size by transport in water.

HYPOTHESES

1. There is no significant difference between the seed size distributions of the life and death assemblages.

2. Differences between the seed size distributions of the life and death assemblages are influenced by any of the following potential taphonomic factors:
   - seed dispersal mode
   - growth form of parent plant
   - location of parent plant at site
   - sorting by transport in water

LOCATION

The site of this study is a small embayment and adjacent hillside on the north side of Fox Point at the Smithsonian Environmental Research Center (SERC) in Edgewater, Maryland (Fig. 1). SERC encompasses 690 acres bordering the Chesapeake Bay and includes several tidal creeks and rivers that feed into the Chesapeake. Over 550 plant

species have been identified from a great variety of habitats at SERC, including hardwood forests, fresh- and saltwater marshes, ponds, and cultivated or abandoned fields (Higman, 1968).

Fox Point is a small promontory of land projecting eastward, separating Fox Creek to the north from Muddy Creek to the south. Fox Creek is a brackish, tidal estuary, approximately 450m long by 200-300m wide. It ends in a dense marsh just to the west of the study site, and to the east is open where it meets Muddy Creek and Rhode River. The study site (Fig. 2) covers approximately 20m by 50m on the north shore of Fox Point, at its western (landward) end. Fox Point is slightly embayed here, and a small strip of marsh projects about 20m across the mouth of the embayment from the east. Because of this configuration, seeds and other debris in the water may be carried up Fox Creek by the rising tide, and a large proportion may be trapped by the large marsh west of the site, or by the small strip of marsh separating the study site from the rest of Fox Creek. In addition, seeds and other debris entering the water from within the study site will tend to remain there, as these will also be trapped by the marsh. This is evidenced by a thick layer of organic-rich, anoxic mud between the marsh and Fox Point that contains a large volume of macroscopic plant debris (leaves, seeds, roots, and wood). There is a small gravel road following the midline of Fox Point, and the land slopes moderately steeply away from the road on either side. Seeds and other material on the

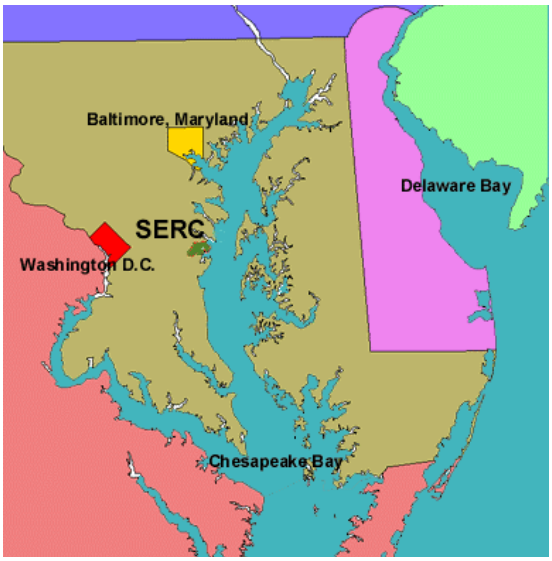

Figure 1 – Map showing the location of the Smithsonian Environmental Research Center (SERC).

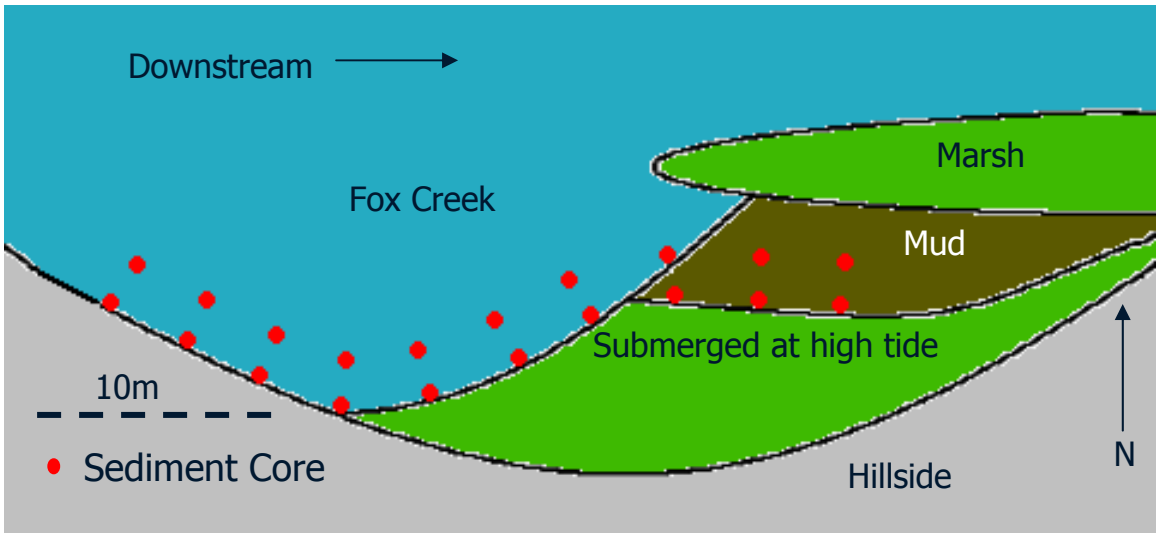

Figure 2 – Map of study site, showing location of sediment cores (red dots). The samples in the more southerly transect are, from west to east: A1, B1, C1, D1, E1, F1, G1, H1, I1, J1. The samples in the more northerly transect are, from west to east: A2, B2, C2, D2, E2, F2, G2, H2, I2, J2.

hillside have the potential to be washed downhill during heavy rains. Because the shoreline and hillside north of the road are concave, there may be a funneling effect, concentrating organic debris from the hillside into a proportionately smaller area than if the hillside were planar.

Offshore, sediment at the site consists of a layer of dense, well-consolidated, pebbly clay, which is overlain by pebbly sand at the western end. The overlying sand grades to a veneer of organic-rich silt and mud which increases in thickness to the east. This organic-rich, anoxic mud is at least 20cm thick at the eastern end of the site. The clay appears to have been reworked, as it contains pebbles and leaf layers, and is poorly sorted. It therefore does not represent Tertiary marine deposition. The presence of recent human artifacts including a bullet and bits of plastic in the sediment cores indicates that deposition has taken place within the past ~50yrs, and the living flora has not changed considerably in at least the past 35yrs. At the time of publication of Higman (1968), vegetation on the hillside at Fox Point was and still is hardwood forest, with a canopy of *Quercus alba, Q. prinus, Q. velutina*, and *Carya tomentosa*. The salt marsh in Fox Creek consisted and still consists primarily of *Spartina cynosuroides* and *S. alterniflora*.

METHODS

Construction of Coring Devices

I built two soft-sediment coring devices with inside core barrel diameters of 6" (15.24cm) and 2" (5.08cm). The 6" diameter corer (Fig. 3) is a slightly modified version of Burnham's (1988) design. The original design calls for welding the handles to a stainless steel core barrel. Instead, I used Schedule 40 PVC pipe for the core barrel and attached the handles by means of threaded flanges, which were bolted to either side of the core barrel. The use of PVC pipe made the corer stronger (stainless steel can buckle under pressure) but has the disadvantages of increasing the weight of the corer (a minor issue) and the thickness of the wall of the core barrel. The latter problem was minimized by filing down the outside bottom edge of the core barrel until it met the inside edge at a low angle, thus sharpening the corer and allowing it to cut through dense sediments and large organic debris.

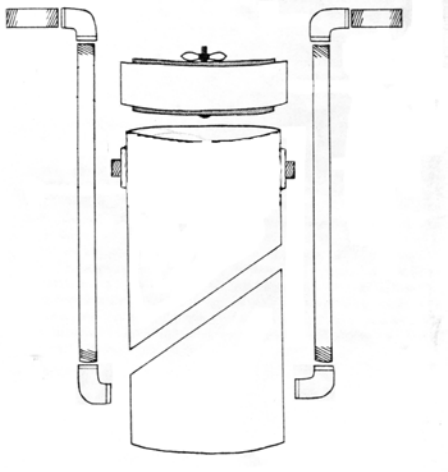

Figure 3 – Schematic of 6" (15.24cm) diameter coring device, modified from Burnham (1988).

The handles and sealing plug follow the original design. Each handle is made of ¾" (1.905cm) galvanized pipe as follows: a male-male adaptor fits into the flange mentioned above. A 90° elbow screws onto the adaptor, so that the long part of the handle, an 18" long pipe, can extend vertically. Another 90° elbow screws onto the end of this pipe, so that the short part of the handle, a 6" (15.24cm) long pipe, can point horizontally away from the corer. I placed a

plastic cap on the end of this piece to protect the user from injury on the sharp, threaded end of the handle. The sealing plug is sold as a single unit, which consists of a rubber gasket between two metal plates. A bolt runs through the center of these plates, with a wing nut at the top. The upper metal plate is larger than the lower, and fits over the top of the core barrel. By tightening the wing nut, the plates compress the rubber gasket, forcing it to expand outwards, thus forming an air- and water-tight seal.

The 2" diameter corer is of a simpler design. The core barrel is also Schedule 40 PVC pipe. The handle, however, is a single 18" (45.72cm) long piece of ¾" galvanized pipe with plastic caps on each end, attached transversely to the core barrel by ring clamps. I used a 2" diameter sealing plug, which is similar to the one mentioned above, except that the metal plates are instead made of plastic.

Both coring devices work in the same way. The core barrel, with the top open, is pushed into the sediment. When the desired depth is reached, the sealing plug is placed on top of the core barrel and the wing nut tightened. When the corer is pulled upward, the suction formed by the column of air and/or water above the sediment serves to keep the sediment core in place. When the seal is released by loosening the wing nut, the sediment core generally falls out of the barrel, and can be caught in a strong plastic bag or other container. In some cases, for instance if the sediment is well consolidated, the sediment core may need to be forced out of the barrel, either by pushing it out with a long stick or by putting one's mouth on the open top of the corer and exhaling forcefully.

Collection of Sediment Cores

I collected a total of twenty samples in two transects consisting of ten samples each (Fig. 2). The first transect (A1-J1) ran roughly west to east, along a line formed by the edge of the water at approximately mid-tide, so that all samples were at the same elevation. I took one sample every three meters. The second transect (A2-J2) ran parallel to the first, with each sample 1.5m offshore (north) from the corresponding sample in the first transect. Each of the 20 samples consists of two sediment cores, one 6" diameter core from which I extracted seeds, and one 2" diameter core for the grain size analysis. At each sample location, I took both cores as close to each other as possible (less than 20cm between the centers of both cores) and to the same depth below the sediment/water interface. None of the cores extend to a depth greater than 20cm below the sediment/water interface. I placed the 6" diameter cores in labeled trash compactor bags and the 2" diameter cores in labeled sealable food storage bags. Collecting the sediment cores is a two-person operation (one to operate the corer and one to catch the core in the sample bag), and I was assisted by Hallie Sims. I collected all of the sediment cores on September 22, 2002.

I used two coring devices of differing size because I felt that a relatively large volume of sediment would be necessary to retrieve a useful number of seeds. Less sediment would be needed for the grain size analysis, and by constructing a 2" diameter corer, I could decrease the volume and weight of the additional cores by a factor of three, making them easier to collect, transport, and store. This was a better alternative to removing a small amount of sediment from a large core for the grain size analysis, because the portion removed would not necessarily be representative of the grain size of

the entire core. It may also have removed seeds that would otherwise have been found in the large core.

Live Plant Species List

The life assemblage consists of all seed plant species (Table 1) living in a roughly 20m by 50m area adjacent to the location of the sediment cores. I defined the northern boundary of the site as the edge of Fox Creek at low tide and the southern boundary as the gravel road at the top of the hillside. The eastern and western boundaries were defined by measuring ten meters to the east and ten meters to the west of the sample transects, and walking uphill perpendicular to the slope until I reached the road. I marked the eastern and western boundaries with yellow tape tied to trees. I included these trees and all seed plants within and along the boundaries in the census. Seeds and fruit on the ground within this area, whether they fell directly from their parent plant or were transported by wind or animal, could roll or be washed by rain downhill into the water. Because the gravel road is at the crest of the hill, seeds and fruit on the south side of the road would be transported into Muddy Creek, thus the road serves as a "natural" boundary.

I further divided the area defined above into three sections: the "Aquatic" section includes all plants growing below the high-tide line of Fox Creek, the "Marginal/Overhanging" section includes all plants growing within one meter upslope from the high-tide line or whose branches extend to directly above the water at high tide, and the "Hillside" section includes all plants between the road and the high-tide line. It should be noted that the "Marginal/Overhanging" section is included within the "Hillside" section.

October 5, 2002, with the assistance of Hallie Sims and Elizabeth Zimmer, I identified as many species of seed plants within the "Hillside" and "Marginal/Overhanging" sections as I could. Due to a very high tide I was unable to access all of the plants in the "Aquatic" section. I returned on October 20, 2002 with Hallie Sims and Thomas Hollowell to complete the census of the "Aquatic" section and to double-check the previous census. Several additional plants were identified in each section and previous misidentifications were corrected. On both dates, we collected samples in a plant press of any plants whose identity we were not entirely sure of, or which bore seeds or fruit. I compared these samples to herbarium specimens at the Smithsonian Institution's National Museum of Natural History (NMNH) in order to confirm their identity, and retained them to assist in the identification of seeds extracted from the sediment cores. I used the following guides to identify the plants at the site: Higman (1968), Brown and Brown (1984, 1999), Petrides and Wehr (1988), Little (1993), Niering and Olmstead (1993), Peterson and McKenny (1996), and Shetler and Orli (2000, 2002). I used nomenclature consistent with that presented in Mabberley (2000). I was unable to identify one out of 41 species at the site. This was a grass (family Gramineae), and was unidentifiable because it lacked an inflorescence. I refer to it here as "unknown grass."

I took note of the growth form of each species at the site, and these fell into five broad categories: herbs, which lack woody tissue; graminoids, which consisted of all Monocots at the site except for *Smilax rotundifolia* (this being a vine); vines, which have

Table 1 – The Life Assemblage. The section(s) in which a given species is found at the site is shown in the third column: H = Hillside, M = Marginal/Overhanging, A = Aquatic. The median seed mass in mg of each species is shown in the sixth column (see Appendix 1 for raw data and calculations), and the source(s) of the seeds weighed to determine this mass is shown in the seventh column: NMNH = herbarium specimens from the National Museum of Natural History, SERC = specimens collected at or near the study site in the Smithsonian Environmental Research Center.

SPECIES	FAMILY	SECTION	GROWTH FORM	DISPERSAL MODE	MEDIAN SEED MASS (mg)	SOURCE
Chimaphila maculata	Ericaceae	H	herb	abiotic	0.00220	NMNH
Pluchea odorata	Compositae	A	herb	abiotic	0.0275	NMNH
Typha angustifolia	Typhaceae	A	graminoid	abiotic	0.0560	NMNH
Rhododendron nudiflorum	Ericaceae	H, M	shrub	abiotic	0.0680	NMNH
Aster tenuifolius	Compositae	A	herb	abiotic	0.082	NMNH
Solidago puberula	Compositae	H, M	herb	abiotic	0.1370	NMNH
Campsis radicans	Bignoniaceae	H, M	vine	abiotic	0.208	NMNH
Vaccinium corymbosum	Ericaceae	H, M	shrub	biotic	0.269	NMNH
Deschampsia flexuosa	Gramineae	H	graminoid	abiotic	0.276	NMNH
Festuca rubra	Gramineae	H	graminoid	abiotic	0.309	NMNH
Vaccinium vacillans	Ericaceae	H, M	shrub	biotic	0.390	NMNH
Hydrocotyle verticillata	Umbelliferae	H, M, A	herb	abiotic	0.450	NMNH
Iva frutescens	Compositae	A	shrub	abiotic	0.729	NMNH
unknown grass	Gramineae	A	graminoid	abiotic	0.730	NMNH+SERC
Panicum virgatum	Gramineae	A	graminoid	abiotic	0.738	NMNH
Teucrium canadense	Labiatae	H, M	herb	abiotic	1.30	NMNH
Atriplex patula	Chenopodiaceae	H, M, A	herb	abiotic	1.438	NMNH
Amaranthus cannabinus	Amaranthaceae	A	herb	abiotic	1.4680	NMNH
Spartina cynosuroides	Gramineae	A	graminoid	abiotic	1.550	NMNH
Spartina alterniflora	Gramineae	A	graminoid	abiotic	1.941	NMNH
Rubus hispidus	Rosaceae	H, M	vine	biotic	2.172	NMNH
Scirpus robustus	Cyperaceae	A	graminoid	abiotic	2.304	SERC
Polygonum punctatum	Polygonaceae	H, M	herb	abiotic	2.743	NMNH
Elymus virginicus	Gramineae	H, M	graminoid	abiotic	3.720	SERC
Liquidambar	Hamamelidaceae	H, M	tree	abiotic	4.690	NMNH

SPECIES	FAMILY	SECTION	GROWTH FORM	DISPERSAL MODE	MEDIAN SEED MASS (mg)	SOURCE
styraciflua						
Juniperus virginiana	Cupressaceae	H	tree	biotic	8.71	NMNH
Rhus radicans	Anacardiaceae	H, M	vine	biotic	9.530	NMNH
Ilex opaca	Aquifoliaceae	H	tree	biotic	14.508	NMNH
Parthenocissus quinquefolia	Vitaceae	H	vine	biotic	14.90	NMNH
Carpinus caroliniana	Betulaceae	H	tree	abiotic	16.96	NMNH
Acer rubrum	Aceraceae	H, M	tree	abiotic	17.768	NMNH
Smilax rotundifolia	Smilacaceae	H, M	vine	biotic	23.86	NMNH
Sassafras albidum	Lauraceae	H	tree	biotic	44.53	NMNH
Fagus grandifolia	Fagaceae	H	tree	biotic	97.10	NMNH
Cornus florida	Cornaceae	H	tree	biotic	101.38	NMNH
Nyssa sylvatica	Cornaceae	H, M	tree	biotic	127.94	NMNH
Quercus alba	Fagaceae	H, M	tree	biotic	723.28	NMNH
Quercus falcata	Fagaceae	H	tree	biotic	821.94	NMNH
Quercus velutina	Fagaceae	H	tree	biotic	1228.5	NMNH
Quercus prinus	Fagaceae	H, M	tree	biotic	1927.09	NMNH
Carya tomentosa	Juglandaceae	H, M	tree	biotic	7091.25	NMNH

woody tissue but rely on other plants for support; shrubs, which have woody tissue and do not reach heights greater than ~4m; and trees, which have woody tissue and can reach heights greater than ~4m. I also assigned each species to one of two categories, depending on the dispersal mode of its seeds. Biotic dispersal involves the intervention of an animal. This includes dispersal by ingestion of the seeds (endozoochory) by any of a variety of dispersers, or seeds which attach to the fur or feathers of a mammal or bird (epizoochory). Abiotic dispersal includes dispersal by wind, water, or seeds which lack an obvious dispersal mechanism (unassisted).

Extraction of Seeds

After all of the sediment cores were collected on September 22, 2002, I transported them to NMNH. I processed all of the samples in a large sink in the Paleobiology Department's rock-cutting laboratory. The procedure I used for extracting seeds from the 6" diameter cores is as follows: I placed a handful of the sample into an 840μm sieve and rinsed the sample with water from a hose attached to the sink's faucet. This removed all sediment particles smaller than coarse sand, as well as very small organic debris. Macroscopic organic debris consisting of leaves, twigs, wood, roots, and

Table 2 – The Death Assemblage. For each taxon/morphotype, the samples in which it was found are shown in the matrix. The numbers "1" and "2" beneath the letters A-J denote the transect. The total number of samples each taxon/morphotype were found in is shown in the right-hand column, and the total species richness of each sample is given in the bottom two rows.

TAXON/MORPHOTYPE	A	B	C	D	E	F	G	H	I	J	# OF CORES:
Eleocharis halophila				2							1
cf. *Aureolaria*						1					1
morphotype 5		2									1
Hydrocotyle				1,2		1	1	1	2	1,2	8
morphotype 7	2			2						2	3
morphotype 12	2	2	2	1	1,2	1,2	2	2	2	1,2	13
morphotype 13	2	2									2
cf. *Bidens*									1		1
morphotype 2									1		1
cf. *Teucrium*				2							1
morphotype 11				1			1				2
Atriplex	1,2	2		2	1	1,2	1,2	1,2	1,2	1,2	15
Amaranthus	2	1,2		1	1,2	1,2	1,2	1,2	1,2	1,2	16
Rubus				2		2	1	1,2	1		6
Scirpus	1,2	1,2		1,2	2	1,2	1,2	1,2	1,2	1	16
Polygonum	1,2	2	1,2	1,2	1,2	1,2	1,2	1,2	1,2	1,2	19
morphotype 14					1						1
cf. *Elymus*							1				1
Liquidambar styraciflua	2					1,2		1,2	1,2	1	8
morphotype 4				2							1
Juniperus virginiana	1,2				2	1,2			1	1	7
morphotype 6						1			1	1	3
Pinus			1				1	1	1	1	5
Rhus radicans		2		1			1			2	4
morphotype 1	1,2		2	1,2			1	1			7
morphotype 3		2		1		2			2	1,2	6
morphotype 8				2		2	2	1		2	5
Ilex opaca	2	2		1	1	1	1	1	2	1	9
Kosteletzkya virginica					1					1	2
Parthenocissus quinquefolia									1	2	2
Carpinus caroliniana	2							1			2
Acer rubrum		2									1
Robinia pseudoacacia				1,2	1,2		2				5
morphotype 10					2	2			1,2	1	5
morphotype 9				2							1
Liriodendron tulipifera	2	2	1,2	1,2	1,2	2	1	1,2	1,2	1,2	16
Cornus amomum									1		1
Lindera benzoin				1							1
Fagus grandifolia	1,2	1	2	1,2	1	1,2	1	1		2	12
Cornus florida	2	2		2	1	1		1			6
Nyssa sylvatica	1,2	1,2	1,2	1,2	1,2	1,2	1	1	1,2	1,2	18
Prunus avium	1,2		1	1,2	2		1	1	1,2	1,2	12
Quercus	2	1,2	1,2	1,2	1,2	1,2	1,2	1,2	1,2	1,2	19
Carya	2			2	1,2						4
Species Richness, Transect 2:	19	15	7	20	12	15	8	9	14	15	
Species Richness, Transect 1:	8	5	6	17	14	15	17	18	18	18	

seeds remained in the sieve. I removed all visible seeds, fruits, and associated structures (i.e.: the cups of acorns [*Quercus*] and beech nuts [*Fagus*]) using tweezers or my fingers and placed them in a small, labeled plastic container. Because the seeds and other organic matter tend to stick to each other in clumps, I also removed small portions of organic matter and after inspecting them for seeds, placed them in a separate labeled plastic container. I continued to rinse, pick out seeds, and remove other organic debris until I had emptied the sieve. I then repeated the process with additional handfuls until the entire sample had been processed before beginning the next sample. This procedure took up to five hours per sample, depending on the amount of organic debris.

When I had processed all 20 samples, I grouped the seeds, fruits, and associated structures from each sample according to morphotype. I identified these to genus or species wherever possible by comparison with samples collected at the site and herbarium specimens at NMNH, as well as photographs and illustrations in Martin and Barkley (1961), Radford, et al. (1968), and Montgomery (1977). I used nomenclature consistent with that presented in Mabberley (2000). I was unable to identify 14 out of a total of 44 morphotypes, and these are designated by the word "Morphotype" followed by a number. Four other morphotypes bore a striking resemblance to the seeds of particular genera, but I am not entirely confident that they do, in fact, belong to these genera. I therefore placed the prefix cf. in front of the genus name. The seeds, fruits, and associated structures I extracted from the sediment cores make up the death assemblage (Table 2).

Weighing of Seeds

For all of the species in the life assemblage, I obtained values for the median seed mass (Table 1) by weighing herbarium specimens at NMNH and/or samples collected at the site. These are all dry weights. Wherever possible, I weighed a total of at least 10 seeds from at least three different specimens of each species. This was not always possible, however, and was limited by the number of herbarium specimens within each species that contain seeds. In general, I attempted to weigh seeds from the Mid-Atlantic States (Maryland, Virginia, Delaware, and North Carolina), in order to account for regional differences in seed mass within a species. Again, this was not always possible, so I used specimens from as near to Maryland as were available. In the case of the "unknown grass," I used the median of all of the values for each species belonging to the family Gramineae.

Because there are a number of different structures that can be called a "seed" in the broadest sense, I weighed only the smallest, indivisible structure that contains a single embryo. I removed the fleshy tissue from berries and drupes, and did not include cups (as in *Fagus* and *Quercus*). I followed these criteria so that the masses would represent the structure most likely to be found in the sediment cores (or in a fossil assemblage). The problem of different structures being called "seeds" is exemplified by the differences between the masses I obtained by weighing specimens and those that I was able to locate in the Seed Information Database of the Royal Botanical Gardens, Kew (Tweddle et al., 2002) (Table 3). The SID values are greater than those that I obtained in every case, and the percent difference ranges from 5.25% (*Acer rubrum*) to 154% (*Fagus grandifolia*). Some of the moderate differences are likely due to the variation in seed mass within

Table 3 – Comparisons of seed mass values from this study (second column) and values from the Seed Information Database (Tweddle et al., 2002; third column) for selected taxa. The percent difference between the values is shown in the right-hand column.

SPECIES	NMNH MEDIAN SEED MASS (mg)	SID MEAN SEED MASS (mg)	% DIFFERENCE
Acer rubrum	17.768	18.7	5.25
Carpinus caroliniana	16.96	33.96	100.2
Cornus florida	101.38	109.1	7.620
Fagus grandifolia	97.10	247	154
Ilex opaca	14.508	16.77	15.60
Juniperus virginiana	8.71	13.03	49.6
Liquidambar styraciflua	4.690	5	7
Nyssa sylvatica	127.94	156.4	22.25
Parthenocissus quinquefolia	14.90	25.3	69.8
Rhus radicans	9.530	14.9	56.3
Rubus hispidus	2.172	2.9	34
Sassafras albidum	44.53	88.96	99.80

species, but the larger differences are probably due to different structures being weighed. For example, the fruit of *Fagus grandifolia* consists of a cup that splits open along four seams, and contains two three-sided nuts. Whereas I used the mass of a single nut, I suspect that the mass reported on the SID is that of the cup and both nuts.

The seed masses for the death assemblage (Table 4) were obtained using the same procedures and criteria as those of the life assemblage. For any species in the death assemblage that is also in the life assemblage, I used the values from the life assemblage. For any seeds identified to genus but not species, for which there is a species in the life assemblage, I again used the values from the life assemblage. In the case of *Quercus*, which is represented by four species in the life assemblage (*Q. alba*, *Q. falcata*, *Q. prinus*, and *Q. velutina*), I used the median of all of the values from all four species. For seeds identified to genus but not species, and for which there are no species in the life assemblage, I used the masses of the species most likely to be found living in the vicinity of the site, which I determined by consulting Higman (1968). For each of the unidentified morphotypes (1-14), I weighed one or more seeds from one of the sediment cores in which they were found. Finally, in the case of the four morphotypes which contain the prefix cf., I used the masses of the corresponding species in the life assemblage, or the species most likely to be found living in the vicinity of the site, which I again determined by consulting Higman (1968). For cf. *Bidens*, I also included the mass of the seed extracted from the sediment core.

I took five repeated measurements of the mass of each specimen for about half of the specimens weighed. This allowed me to determine the uncertainty in the balance used. The largest value of 2σ obtained was that for *Carya tomentosa*, U.S. National Herbarium specimen 2112D, where $2\sigma = 0.55$mg. Not coincidentally, this was also the specimen with the greatest mass of any that I weighed. Since $2\sigma = 0.55$mg is therefore an upper limit, I used this value for all specimens for which I did not take multiple measurements. Many of the specimens weighed contained more than one seed, so I divided the mean total mass and 2σ values for each specimen by the number of seeds weighed. Finally, for each species or morphotype in the life and death assemblages, I

Table 4 – The Death Assemblage. The family (where known) is shown in the second column. The median seed mass for each taxon/morphotype is shown in the middle column, and the source(s) of the seeds weighed to determine this mass is shown in the right-hand column: NMNH and SERC as in Table 1; Core = seeds extracted from sediment cores collected at the site.

TAXON/MORPHOTYPE	FAMILY	MEDIAN SEED MASS (mg)	SOURCE
Eleocharis halophila	Cyperaceae	0.342	NMNH
cf. *Aureolaria*	Scrophulariaceae	0.3433	NMNH
morphotype 5		0.380	Core
Hydrocotyle	Umbelliferae	0.450	NMNH
morphotype 7		0.60	Core
morphotype 12		0.696	Core
morphotype 13		0.80	Core
cf. *Bidens*	Compositae	0.973	NMNH+Core
morphotype 2		1.06	Core
cf. *Teucrium*	Labiatae	1.30	NMNH
morphotype 11		1.32	Core
Atriplex	Chenopodiaceae	1.438	NMNH
Amaranthus	Amaranthaceae	1.4680	NMNH
Rubus	Rosaceae	2.172	NMNH
Scirpus	Cyperaceae	2.304	SERC
Polygonum	Polygonaceae	2.743	NMNH
morphotype 14		3.48	Core
cf. *Elymus*	Gramineae	3.720	SERC
Liquidambar styraciflua	Hamamelidaceae	4.690	NMNH
morphotype 4		7.94	Core
Juniperus virginiana	Cupressaceae	8.71	NMNH
morphotype 6		9.08	Core
Pinus	Pinaceae	9.367	NMNH
Rhus radicans	Anacardiaceae	9.530	NMNH
morphotype 1		9.850	Core
morphotype 3		11.12	Core
morphotype 8		13.780	Core
Ilex opaca	Aquifoliaceae	14.508	NMNH
Kosteletzkya virginica	Malvaceae	14.6	Core+SERC
Parthenocissus quinquefolia	Vitaceae	14.90	NMNH
Carpinus caroliniana	Betulaceae	16.96	NMNH
Acer rubrum	Aceraceae	17.768	NMNH
Robinia pseudoacacia	Leguminosae	17.892	NMNH
morphotype 10		26.453	Core
morphotype 9		30.52	Core
Liriodendron tulipifera	Magnoliaceae	31.038	NMNH
Cornus amomum	Cornaceae	43.7008	NMNH
Lindera benzoin	Lauraceae	64.64	NMNH+Core
Fagus grandifolia	Fagaceae	97.10	NMNH
Cornus florida	Cornaceae	101.38	NMNH
Nyssa sylvatica	Cornaceae	127.94	NMNH
Prunus avium	Rosaceae	171.320	NMNH
Quercus	Fagaceae	1228.5	NMNH
Carya	Juglandaceae	7091.25	NMNH

used the median value of the mean masses per seed of all specimens within that species. I used the median rather than the mean value because the median is less sensitive to outliers. Although there is a seemingly large variability in seed mass within species, it is generally within an order of magnitude. This is small compared to the variation between species in a given flora of up to six orders of magnitude (Westoby et al., 1992), as is the case with the living flora at the site. See Appendix 1 for the raw data and calculations used.

Grain Size Analysis

I have determined the grain size distributions of four out of the 20 2" diameter sediment cores. The four samples (A1, D1, G1, and J1) are all from the first (near-shore) transect, and are spaced 9m apart. I chose these four to be representative of the change in grain size and character from the western end to the eastern end of the sample transects. I used the same procedure for all four samples. First, if the sample size was too large, I cut down the size of the sample while making sure that it was still representative of the entire core. I did this by lumping the sediment into a pile, cutting the pile into four quarters, removing two opposite quarters and lumping the remaining two opposite quarters together. I repeated this until a desirable sample size was reached.

I removed the large organic debris (where present) from each samples by rinsing the sample through a 2mm sieve and picking out the organic debris by hand. The remaining sediment in the sieve was placed along with the particles smaller than 2mm in diameter into a 1000mL beaker. I then allowed the sediment in the beakers to settle for at least 20hrs or centrifuged the sample at ~2000rpm for 30min, before decanting and discarding as much of the water as possible without losing any sediment. In order to remove the majority of the smaller organic particles, I added undiluted Clorox to each of the beakers up to the 750mL mark, stirred the sediment thoroughly, and allowed it to settle and react for at least 20hrs. I decanted and discarded the Clorox, taking care not to lose any sediment, and, if necessary, repeated with more Clorox. Otherwise, I added distilled water to the 750mL mark, allowed the sediment to settle for at least 20hrs or centrifuged the sample at ~2000rpm for 30min, decanted the water, and repeated one more time with another distilled water rinse.

After I had removed most of the organic matter, I placed each sample into a pre-weighed beaker, which was then placed in an oven at ~60°C until the sample was completely dry. I then recorded the weight of the beaker plus the dry sample. By subtracting the weight of the empty beaker from the weight of the beaker plus the dry sample, I calculated the total dry weight of each sediment sample. I rinsed each sample through a series of sieves at increments of 1Φ, starting with -1.0Φ (2000μm), then 0.0Φ (1000μm), 1.0Φ (500μm), 2.0Φ (250μm), 3.0Φ (125μm), and finally 4.0Φ (62.5μm). Particles smaller than 4.0Φ were caught in a bucket or buckets. I then placed each size fraction into a pre-weighed beaker, which I placed in an oven at ~60°C until dry. I weighed each of the beakers containing the different size fractions from each sample, and subtracted the weights of the empty beakers to obtain the dry weight of each of the size fractions (Appendix 2).

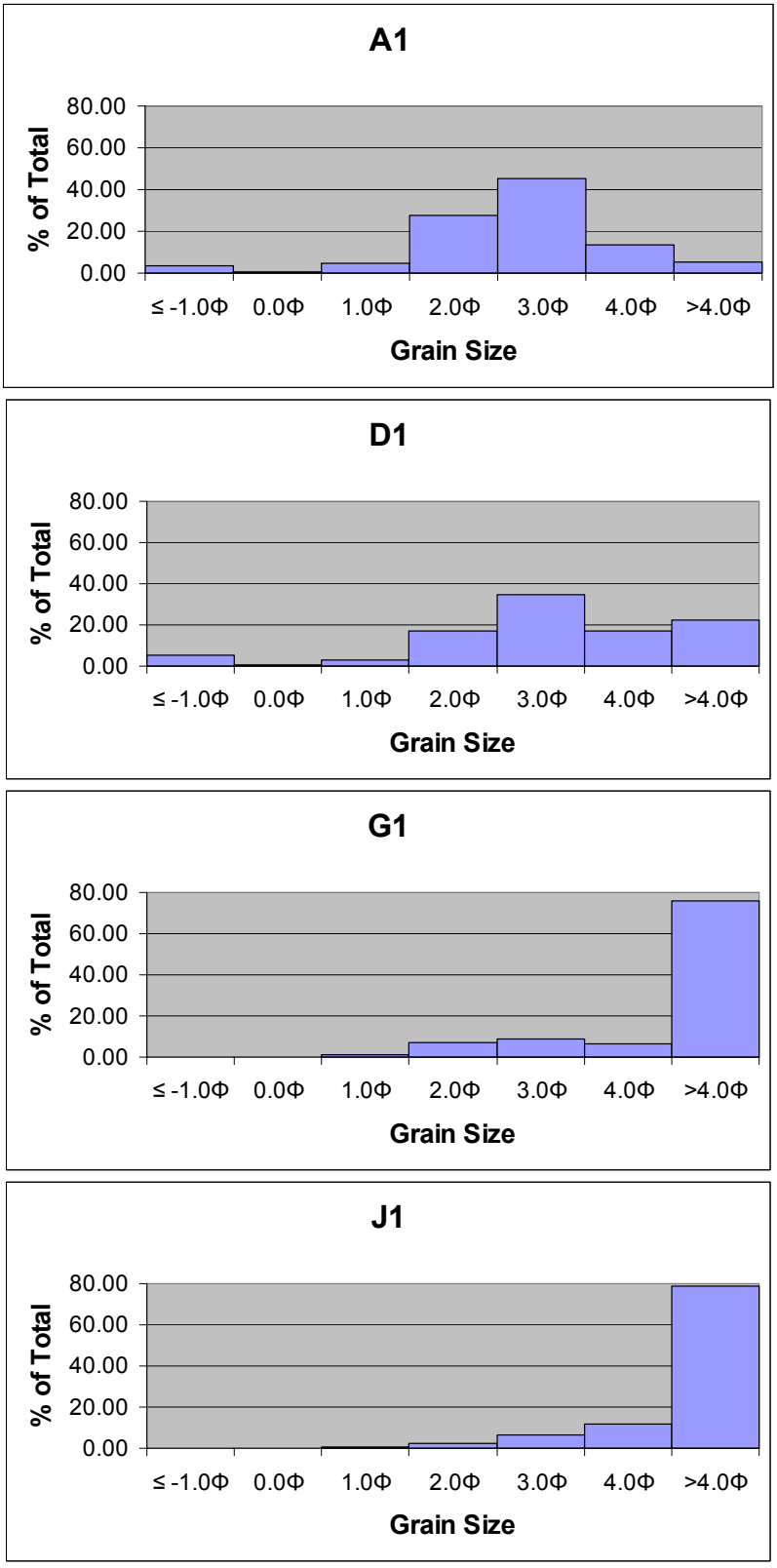

Figure 4 – Histograms of grain size of four representative samples (A1, D1, G1, J1).

Because some amount of each sample was lost, I added up the masses of the different fractions in each sample, and expressed each fraction within a sample as a percentage of this total. I then plotted histograms (Fig. 4) and cumulative percent distributions (Fig. 5) for each of the four samples. I read the percentiles Φ_5, Φ_{16}, Φ_{25}, Φ_{50}, Φ_{75}, Φ_{86}, and Φ_{95} off of the cumulative percent distributions, and calculated the mean, standard deviation, median and sorting index for each sample. The mean is given by $(\Phi_{16} + \Phi_{50} + \Phi_{84})/3$; the standard deviation by $(\Phi_{84} - \Phi_{16})/2$; the median is simply Φ_{50}; and the sorting index is given by $(\Phi_{84} - \Phi_{16})/4 + (\Phi_{95} - \Phi_5)/6.6$. These statistics are reported in Table 5.

Table 5 – Grain Size Data. Φ percentiles and standard measures for grain size distributions of four representative samples (A1, D1, G1, J1).

SAMPLE:	A1	D1	G1	J1
Φ_5:	-0.2	-1.5	0.9	1.8
Φ_{16}:	0.8	1.0	2.4	3.0
Φ_{25}:	1.1	1.5	3.6	3.5
Φ_{50}:	1.8	2.2	3.8	3.8
Φ_{75}:	2.5	3.5	4.1	4.2
Φ_{84}:	2.7	3.8	4.3	4.3
Φ_{95}:	3.8	4.3	4.4	4.4
Mean:	1.8	2.3	3.5	3.7
Std. Dev.:	1.0	1.4	1.0	0.7
Median:	1.8	2.2	3.8	3.8
Sorting:	1.1	1.6	1.0	0.7

Statistical Analyses

I compared different combinations of the life and death assemblages and subsets thereof (see Appendix 3 for histograms of these). I used nonparametric tests in all cases because for many of these subsets the data are not normally distributed (Sokal and Rohlf, 1995). In order to determine if there is a significant difference between the seed size distributions of two subsets, I used the Mann-Whitney U-test. To determine if there is a significant difference between the seed size distributions of more than two subsets, I used the Kruskal-Wallis test. The null hypothesis for both of these tests is that the subsets compared have the same distribution of values (seed mass in this case). Both tests work by ranking all of the data together, and comparing the mean ranks of the different subsets. In the case of tied ranks, the average rank is used for each of the tied values. The output of both tests is a P-value. If $P \leq 0.05$, the subsets compared are significantly different (95% confidence interval). I used Statview for all analyses.

RESULTS

I used the Mann-Whitney U-test to determine whether or not there is a significant difference between the seed size distributions of the life assemblage and the death assemblage (pooled data from all 20 samples). The resulting P-value is 0.1259. Thus, there is no significant difference between the two distributions. I also performed the Kruskal-Wallis test using the life assemblage and each of the 20 sediment cores considered as a discreet sample. The P-value for this test is 0.5728. This is also not a significant difference, consistent with the results above.

Within the death assemblage, I performed Kruskal-Wallis tests for different groups of sediment cores. There is no significant difference among all 20 samples (P = 0.9173), among the samples in the first transect (samples A1-J1, P = 0.7158), or among samples in the second transect (samples A2-J2, P = 0.8766). Likewise, there is no significant difference between the seed size distributions of the samples in the western

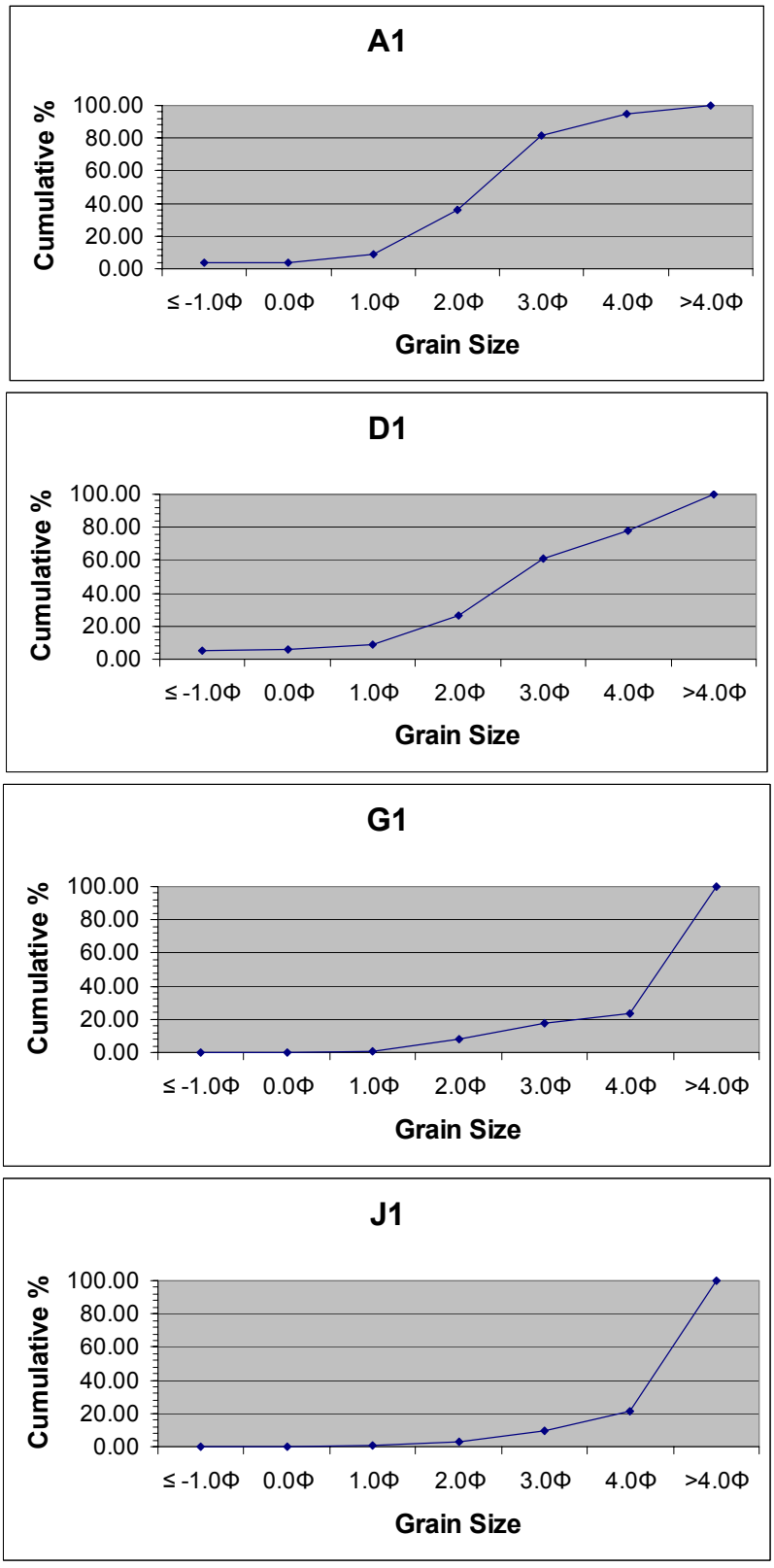

Figure 5 – Cumulative percent distributions of grain size of four representative samples (A1, D1, G1, J1).

half of the site (samples A1-E1 and A2-E2, P = 0.8326), or in the eastern half of the site (samples F1-J1 and F2-J2, P = 0.9738). I also used the Mann-Whitney U-test to compare the pooled data from the western half of the site with the pooled data from the eastern half of the site (as though each half were one large sample). The resulting P-value for this comparison is 0.9129, which is not significantly different.

I compared the seed size distributions of different growth forms (herbs/graminoids, shrubs/vines, and trees) within the life assemblage using a Kruskal-Wallis test. The result is $P < 0.0001$, which indicates that there is a significant difference in the seed size distributions of different growth forms at the site. There is also a significant difference ($P = 0.0401$, from Kruskal-Wallis test) between the seed size distributions of different locations (Hillside, Marginal/Overhanging, and Aquatic) within the life assemblage. The seed size distributions of different dispersal modes (biotic and abiotic) within the life assemblage are also significantly different ($P < 0.0001$, from Mann-Whitney U-test).

I performed Mann-Whitney U-tests using the pooled data from all 20 samples of the death assemblage and different locations, growth forms, and dispersal modes within the life assemblage. There is no significant difference between the seed size distributions of the death assemblage and the Hillside ($P = 0.7879$) or Marginal/Overhanging ($P = 0.3049$) sections of the life assemblage. There is, however, a significant difference ($P = 0.0004$) between the death assemblage and the Aquatic section of the life assemblage. There are significant differences between the death assemblage and each of the growth forms (herbs/graminoids, $P < 0.0001$; shrubs/vines, $P = 0.0340$; and trees, $P = 0.0006$) in the life assemblage. Likewise, there are significant differences between the death assemblage and both of the dispersal modes (biotic, $P = 0.0197$; and abiotic, $P < 0.0001$) within the life assemblage. See Table 6 for a summary of the results of the statistical analyses.

The mean grain size of the four samples analyzed decreases in diameter (increases in Φ value) from west to east across the site. However, there is no overall trend in seed size from the western end to the eastern end of the site. There is therefore no clear evidence of sorting of the seeds by transport in the water.

DISCUSSION

The lack of a significant difference between the seed size distributions of the life and death assemblages used in this study lends support to the utility of seed size distributions from fossil assemblages in paleoecological and paleoclimatological reconstruction and interpretation. As always, however, care should still be taken that the fossil seed assemblages used are not obviously biased in terms of paleogeographic location, depositional environment, or sampling method, and that the sample size is sufficiently large. Although the life and death assemblages are not significantly different, the P-value ($P = 0.1259$) is relatively small, and it remains to be seen if similar experiments performed in different vegetation types and depositional environments would yield the same result.

Although the seed size distributions of different dispersal modes are significantly different from each other, it is not possible to determine from the seed size information alone if one dispersal mode has been preferentially incorporated into the death assemblage to a large extent, because the death assemblage is significantly different from both dispersal modes. The P-value for the comparison of the death assemblage and seeds

Table 6 – Statistical Analyses. The distributions being compared in each analysis are shown in the left-hand column, and the test used to compare them in the second column. The number of tied ranks is shown in the third column, and the corrected P-value in the right-hand column.

DISTRIBUTIONS COMPARED	TEST USED	# OF TIES	P-VALUE
Life assemblage, death assemblage (pooled data)	Mann-Whitney U-test	20	0.1259
Life assemblage, all 20 cores (A1-J1 and A2-J2)	Kruskal-Wallis	33	0.5728
All 20 cores (A1-J1 and A2-J2)	Kruskal-Wallis	31	0.9173
Transect 1 (A1-J1)	Kruskal-Wallis	25	0.7158
Transect 2 (A2-J2)	Kruskal-Wallis	25	0.8766
Western half (A1-E1 and A2-E2)	Kruskal-Wallis	21	0.8326
Eastern half (F1-J1 and F2-J2)	Kruskal-Wallis	24	0.9738
Pooled western half (A1-E1 and A2-E2), pooled eastern half (F1-J1 and F2-J2)	Mann-Whitney U-test	27	0.9129
Herbs/graminoids, shrubs/vines, trees	Kruskal-Wallis	0	< 0.0001
Hillside, Marginal/Overhanging, Aquatic	Kruskal-Wallis	19	0.0401
Biotic, Abiotic	Mann-Whitney U-test	0	< 0.0001
Death assemblage (pooled data), Hillside	Mann-Whitney U-test	18	0.7879
Death assemblage (pooled data), Marginal/Overhanging	Mann-Whitney U-test	11	0.3049
Death assemblage (pooled data), Aquatic	Mann-Whitney U-test	4	0.0004
Death assemblage (pooled data), herbs/graminoids	Mann-Whitney U-test	6	< 0.0001
Death assemblage (pooled data), shrubs/vines	Mann-Whitney U-test	3	0.0340
Death assemblage (pooled data), trees	Mann-Whitney U-test	10	0.0006
Death assemblage (pooled data), biotic	Mann-Whitney U-test	10	0.0197
Death assemblage (pooled data), abiotic	Mann-Whitney U-test	10	< 0.0001

from the life assemblage with biotic dispersal ($P = 0.0197$) is larger than that for seeds within the life assemblage with abiotic dispersal ($P < 0.0001$), but this may be due more to a lack of seeds smaller than 0.342mg (median species mass) in the death assemblage than to a bias towards biotically dispersed seeds.

Similarly, the three different growth form categories within the life assemblage that I compared have seed size distributions that are significantly different from each other. Again, however, none of the growth forms appear to be greatly overrepresented in the death assemblage from seed size data alone, as the seed size distribution of the death assemblage is significantly different from all three dispersal modes.

The seed size distributions of different locations within the life assemblage (Hillside, Marginal/Overhanging, and Aquatic) are all significantly different from each other. The death assemblage is not significantly different from either the Hillside or Marginal/Overhanging sections, but is significantly different from the Aquatic section. This latter difference is most likely due to a lack of small seeds in the death assemblage. Plants living in the salt marsh or below the high tide line at the site are underrepresented in the death assemblage relative to plants living on the adjacent hillside. This bias may have been introduced as a consequence of the methods I used in this study. In particular, because I used an 840μm sieve while extracting seeds from the sediment cores, seeds with a diameter less than 840μm may have been lost. Likewise, small seeds may have been overlooked as I used only my eyesight to locate seeds in the sediment cores. Therefore, there may have been seeds present in the sediment cores that were smaller than 0.342mg, but none were found. This is a possible reason for the difference between the seed size distributions of the Aquatic section of the life assemblage and the overall death assemblage.

FUTURE WORK

I will complete the grain size analyses of the remaining sediment cores in order to better assess the correlation (or lack thereof) between seed size and grain size distributions among the sediment cores. I will also examine the relationships between degradation of seeds and sediment size/type. Additionally, I will be conducting further analyses of the data collected in this study in order to examine the effects of sample size on the death assemblage.

This study is admittedly limited in scope. Only one vegetation type in one depositional environment has been examined. Seeds in the fossil record come from many different vegetation types and depositional environments, and the fidelity of seed size distributions in potential fossil assemblages to those of their source communities remains to be examined in the majority of these environments. Although the results of this study are encouraging with regards to seed size distributions from tidal estuary deposits, they cannot be extended to include other depositional environments until similar studies have been performed in them.

CONCLUSIONS

The fidelity of seed size distributions from fossil assemblages to those of their source communities is relatively strong in the case of hardwood forests growing alongside tidal estuaries, but requires further testing in other vegetation types and depositional environments. There does not appear to be any significant bias for or against the burial of particular growth forms or seed dispersal modes at the study site described in this paper. There does appear to be a bias against the preservation of the seeds of plants growing below the high tide line, but this may be a consequence of the collection methods used. There is no evidence that transport in water has sorted the seeds according to size at this site.

ACKNOWLEDGEMENTS

I would like to thank my advisors, Julio Friedmann and Hallie Sims, for their comments, criticism, and suggestions, and especially for their encouragement. The following people also provided assistance in identification of plants and seeds; access to laboratories and equipment; comments and suggestions for the project, thesis, and presentations; etc.: Ashley Allen, Bill Boykins, Phil Candela, Vicki Funk, Bob Gastaldo, Mark Haddon, Tom Hollowell, Thomas Holtz, Jay Kaufman, Conrad Labandeira, Skip Lyles, Ian McIntyre, John Merck, Paul Peterson, Harold Robinson, Rob Soreng, Mark Strong, Tab Tesnau, Denis Whigham, Scott Wing, and Elizabeth Zimmer.

I would also like to thank Jeffrey and Lily Chen for their generous donation to the scholarship that bears their names, of which I am a proud recipient. Were it not for their generosity I would not have had anywhere near as much time to work on this project as I have had.

Funding for materials and transportation came from the Smithsonian Institution's Evolution of Terrestrial Ecosystems Program.

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APPENDIX 1

Seed Mass Data

The number of seeds, mean total mass (mg), standard deviation of the mean total mass (mg), mean weight per seed (mg), and standard deviation of the mean weight per seed (mg) for each specimen of each taxon/morphotype weighed are shown in columns two through five. The median weight per seed (mg) of each taxon/morphotype is given in the right-hand column.

Species	# of seeds	Mean total mass (mg)	± 2σ (mg)	Mean wt/ seed (mg)	± 2σ (mg)	Median wt/ seed (mg)
Acer rubrum	2	15.1	0.00	7.55	0.00	17.768
	3	58.70	0.14	19.567	0.047	
	5	88.84	0.11	17.768	0.022	
Amaranthus cannabinus	15	20.34	0.11	1.3560	0.0073	1.4680
	15	23.70	0.14	1.5800	0.0094	
Rhus radicans	10	103.880	0.089	10.3880	0.0089	9.530
	10	86.72	0.26	8.672	0.026	
Ilex opaca	4	52.56	0.18	13.140	0.045	14.508
	4	63.50	0.24	15.875	0.061	
	4	50.82	0.17	12.705	0.042	
	8	154.46	0.11	19.308	0.014	
Carpinus caroliniana	7	123.40	0.55	17.629	0.079	16.96
	3	48.90	0.55	16.30	0.18	
Campsis radicans	40	8.30	0.55	0.208	0.014	0.208
Atriplex patula	10	10.10	0.55	1.010	0.055	1.438
	15	28.00	0.55	1.867	0.037	
Aster tenuifolius	21	1.04	0.11	0.050	0.005	0.082
	20	2.30	0.14	0.115	0.007	
Bidens polylepis	6	5.84	0.11	0.973	0.018	0.973
	8	6.36	0.11	0.795	0.014	
cf. *Bidens*	1	1.04	0.11	1.04	0.11	
Iva fructescens	8	8.12	0.17	1.015	0.021	0.729
	20	8.86	0.27	0.443	0.013	
Pluchea odorata	40	1.10	0.14	0.0275	0.0035	0.0275
Solidago puberula	10	1.34	0.11	0.1340	0.011	0.1370
	10	1.40	0.14	0.1400	0.014	
Cornus amomum	5	191.22	0.17	38.2440	0.033	43.7008
	8	393.26	0.11	49.1575	0.014	
Cornus florida	4	288.40	0.55	72.10	0.14	101.38
	4	522.60	0.55	130.65	0.14	
Nyssa sylvatica	2	266.20	0.55	133.10	0.28	127.94
	8	982.20	0.55	122.775	0.069	
Juniperus virginiana	8	69.70	0.55	8.713	0.069	8.71
	3	33.20	0.55	11.07	0.18	
	3	16.20	0.55	5.40	0.18	
Eleocharis halophila	10	3.42	0.17	0.342	0.017	0.342
Scirpus robustus	23	53.00	0.55	2.304	0.024	2.304
Chimaphila maculata	1000	2.20	0.55	0.00220	0.00055	0.00220
Rhododendron nudiflorum	16	0.86	0.11	0.0538	0.0068	0.0680

Species	# of seeds	Mean total mass (mg)	± 2σ (mg)	Mean wt/ seed (mg)	± 2σ (mg)	Median wt/ seed (mg)
	35	2.88	0.17	0.0823	0.0048	
Vaccinium corymbosum	18	4.90	0.55	0.272	0.031	0.269
	15	4.00	0.55	0.267	0.037	
Vaccinium vacillans	20	7.00	0.55	0.350	0.028	0.390
	20	8.60	0.55	0.430	0.028	
Fagus grandifolia	4	300.60	0.55	75.15	0.14	97.10
	2	194.20	0.55	97.10	0.28	
	4	449.50	0.55	112.38	0.14	
Quercus alba	5	3616.40	0.55	723.28	0.11	723.28
	3	1857.90	0.55	619.30	0.18	1228.5
	2	4246.20	0.55	2123.10	0.28	
Quercus falcata	5	4109.70	0.55	821.94	0.11	821.94
	1	289.60	0.55	289.60	0.55	
	3	3025.60	0.55	1008.53	0.18	
Quercus prinus	2	4556.90	0.55	2278.45	0.28	1927.09
	1	1480.20	0.55	1480.20	0.55	
	3	4727.20	0.55	1575.73	0.18	
	3	9112.20	0.55	3037.40	0.18	
Quercus velutina	2	1767.90	0.55	883.95	0.28	1228.5
	2	2307.50	0.55	1153.75	0.28	
	2	2795.40	0.55	1397.70	0.28	
	3	3909.70	0.55	1303.23	0.18	
Deschampsia flexuosa	35	6.60	0.55	0.189	0.016	0.276
	30	10.90	0.55	0.363	0.018	0.730
Elymus virginicus	10	37.20	0.14	3.720	0.014	3.720
Festuca rubra	200	34.20	0.55	0.1710	0.0028	0.309
	21	9.40	0.55	0.448	0.026	
Panicum virgatum	20	14.90	0.55	0.745	0.028	0.738
	30	21.90	0.55	0.730	0.018	
Spartina alterniflora	17	33.00	0.55	1.941	0.032	1.941
Spartina cynosuroides	20	31.00	0.55	1.550	0.028	1.550
Liquidambar styraciflua	25	137.00	0.55	5.480	0.022	4.690
	25	97.50	0.55	3.900	0.022	
Carya tomentosa	2	15445.60	0.55	7722.80	0.28	7091.25
	2	16425.82	0.55	8212.91	0.28	
	1	5503.20	0.55	5503.20	0.55	
	1	6459.70	0.55	6459.70	0.55	
Teucrium canadense	4	5.20	0.55	1.30	0.14	1.30
	11	19.80	0.55	1.800	0.050	
	5	6.00	0.55	1.20	0.11	
Lindera benzoin	3	364.44	0.18	121.480	0.060	64.64
	3	132.28	0.17	44.093	0.056	
	1	64.64	0.11	64.64	0.11	
Sassafras albidum	3	124.80	0.55	41.60	0.18	44.53
	2	94.90	0.55	47.45	0.28	
Robinia pseudoacacia	9	187.74	0.23	20.860	0.025	17.892
	17	253.70	0.20	14.924	0.012	
Liriodendron tulipifera	16	593.70	0.55	37.106	0.034	31.038

Species	# of seeds	Mean total mass (mg)	± 2σ (mg)	Mean wt/ seed (mg)	± 2σ (mg)	Median wt/ seed (mg)
	20	499.40	0.55	24.970	0.028	
Kosteletzkya virginica	1	20.72	0.15	20.72	0.15	14.6
	1	8.08	0.15	8.08	0.15	
	2	29.28	0.15	14.640	0.075	
Pinus virginiana	12	93.40	0.55	7.783	0.046	9.367
	20	219.00	0.55	10.950	0.028	
Polygonum puctatum	15	29.00	0.55	1.933	0.037	2.743
	15	53.30	0.55	3.553	0.037	
Prunus avium	1	275.24	0.23	275.24	0.23	171.320
	2	111.70	0.14	55.850	0.071	
	1	171.32	0.17	171.32	0.17	
Rubus hispidus	10	19.70	0.55	1.970	0.055	2.172
	15	35.60	0.55	2.373	0.037	
Aureolaria flava	80	27.46	0.18	0.3433	0.0022	0.3433
Smilax rotundifolia	1	33.60	0.55	33.60	0.55	23.86
	8	113.00	0.55	14.125	0.069	
Typha angustifolia	100	5.60	0.55	0.0560	0.0055	0.0560
Hydrocotyle verticillata	15	3.60	0.55	0.240	0.037	0.450
	10	6.60	0.55	0.660	0.055	
Parthenocissus quinquefolia	6	89.40	0.55	14.900	0.092	14.90
	5	86.40	0.55	17.28	0.11	
	2	19.00	0.55	9.50	0.28	
morphotype 1	2	19.70	0.14	9.850	0.071	9.850
morphotype 2	1	1.06	0.11	1.06	0.11	1.06
morphotype 3	1	11.12	0.17	11.12	0.17	11.12
morphotype 4	1	7.94	0.11	7.94	0.11	7.94
morphotype 5	1	0.380	0.089	0.380	0.089	0.380
morphotype 6	1	9.08	0.17	9.08	0.17	9.08
morphotype 7	1	0.60	0.14	0.60	0.14	0.60
morphotype 8	1	13.780	0.089	13.780	0.089	13.780
morphotype 9	2	61.04	0.23	30.52	0.11	30.52
morphotype 10	3	79.36	0.18	26.453	0.060	26.453
morphotype 11	1	1.32	0.17	1.32	0.17	1.32
morphotype 12	5	3.48	0.17	0.696	0.033	0.696
morphotype 13	1	0.80	0.14	0.80	0.14	0.80
morphotype 14	1	3.5	0.17	3.48	0.17	3.48

APPENDIX 2

Grain Size Data

Each of the four following tables shows the grain size data for one of the four representative samples analyzed (A1, D1, G1, J1). The object weighed is shown in the left-hand column; the mean and standard deviation of five repeated measurements are shown in the second and third columns, respectively; the percentage of the sum of the different size fractions is shown in the fourth column; and the cumulative percent is shown in the right-hand column.

SAMPLE A1	MEAN (g):	2σ (g):	% OF TOTAL FRACTIONS:	CUMULATIVE %:
empty beaker A:	408.54	0.01		
beaker A + initial sample:	494.70	0.01		
initial sample:	86.16	0.01	100.65	
empty beaker B:	79.83	0.01		
beaker B + ≤ -1.0Φ:	82.70	0.01		
≤ -1.0Φ:	2.87	0.02	3.35	3.35
empty beaker C:	89.37	0.01		
beaker C + 0.0Φ:	89.95	0.01		
0.0Φ:	0.59	0.02	0.69	4.04
empty beaker D:	85.46	0.01		
beaker D + 1.0Φ:	89.32	0.00		
1.0Φ:	3.86	0.01	4.50	8.54
empty beaker E:	154.30	0.01		
beaker E + 2.0Φ:	178.04	0.01		
2.0Φ:	23.74	0.01	27.73	36.28
empty beaker F:	181.29	0.01		
beaker F + 3.0Φ:	220.13	0.01		
3.0Φ:	38.84	0.01	45.38	81.66
empty beaker G:	192.79	0.01		
beaker G + 4.0Φ:	204.15	0.01		
4.0Φ:	11.35	0.01	13.26	94.92
empty beaker H:	397.96	0.01		
beaker H + >4.0Φ:	402.30	0.01		
>4.0Φ:	4.35	0.02	5.08	100.00
total fractions:	85.60		100.00	

SAMPLE D1	MEAN (g):	2σ (g):	% OF TOTAL FRACTIONS:	CUMULATIVE %:
empty beaker A:	303.05	0.01		
beaker A + initial sample:	461.91	0.01		
initial sample:	158.86	0.01	104.16	
empty beaker B:	79.83	0.01		
beaker B + ≤ -1.0Φ:	88.12	0.01		
≤ -1.0Φ:	8.29	0.02	5.44	5.44
empty beaker C:	89.37	0.01		
beaker C + 0.0Φ:	90.43	0.01		
0.0Φ:	1.07	0.02	0.70	6.14
empty beaker D:	76.36	0.01		
beaker D + 1.0Φ:	80.78	0.01		

SAMPLE D1	MEAN (g):	2σ (g):	% OF TOTAL FRACTIONS:	CUMULATIVE %:
1.0Φ:	4.41	0.01	2.89	9.03
empty beaker E:	75.47	0.01		
beaker E + 2.0Φ:	101.52	0.00		
2.0Φ:	26.05	0.01	17.08	26.11
empty beaker F:	216.82	0.01		
beaker F + 3.0Φ:	269.70	0.01		
3.0Φ:	52.88	0.01	34.67	60.78
empty beaker G:	305.00	0.00		
beaker G + 4.0Φ:	330.68	0.01		
4.0Φ:	25.68	0.01	16.84	77.62
empty beaker H:	303.12	0.01		
beaker H + >4.0Φ:	337.26	0.01		
>4.0Φ:	34.14	0.02	22.38	100.00
total fractions:	152.52		100.00	

SAMPLE G1	MEAN (g):	2σ (g):	% OF TOTAL FRACTIONS:	CUMULATIVE %:
empty beaker A:	273.99	0.01		
beaker A + initial sample:	282.53	0.02		
initial sample:	8.54	0.02	132.50	
empty beaker B:				
beaker B + ≤ -1.0Φ:				
≤ -1.0Φ:			0.00	0.00
empty beaker C:	89.36	0.01		
beaker C + 0.0Φ:	89.37	0.01		
0.0Φ:	0.01	0.02	0.16	0.16
empty beaker D:	76.36	0.01		
beaker D + 1.0Φ:	76.42	0.01		
1.0Φ:	0.06	0.02	0.93	1.09
empty beaker E:	75.47	0.01		
beaker E + 2.0Φ:	75.94	0.01		
2.0Φ:	0.47	0.01	7.29	8.38
empty beaker F:	216.81	0.01		
beaker F + 3.0Φ:	217.40	0.01		
3.0Φ:	0.58	0.02	9.03	17.41
empty beaker G:	305.00	0.01		
beaker G + 4.0Φ:	305.41	0.01		
4.0Φ:	0.42	0.01	6.46	23.87
empty beaker H:	274.01	0.01		
beaker H + >4.0Φ:	278.91	0.01		
>4.0Φ:	4.91	0.01	76.13	100.00
total fractions:	6.44		100.00	

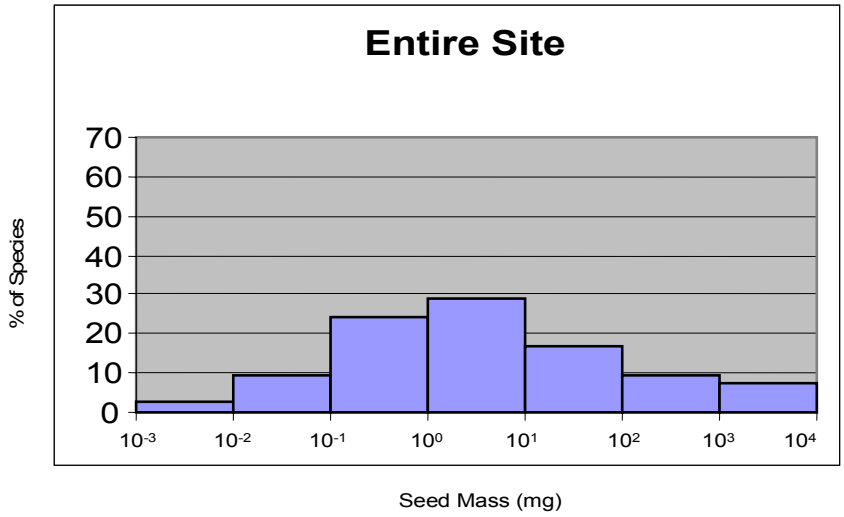
SAMPLE J1	MEAN (g):	2σ (g):	% OF TOTAL FRACTIONS:	CUMULATIVE %:
empty beaker A:	408.57	0.01		
beaker A + initial sample:	423.48	0.01		
initial sample:	14.91	0.01	123.33	
empty beaker B:				

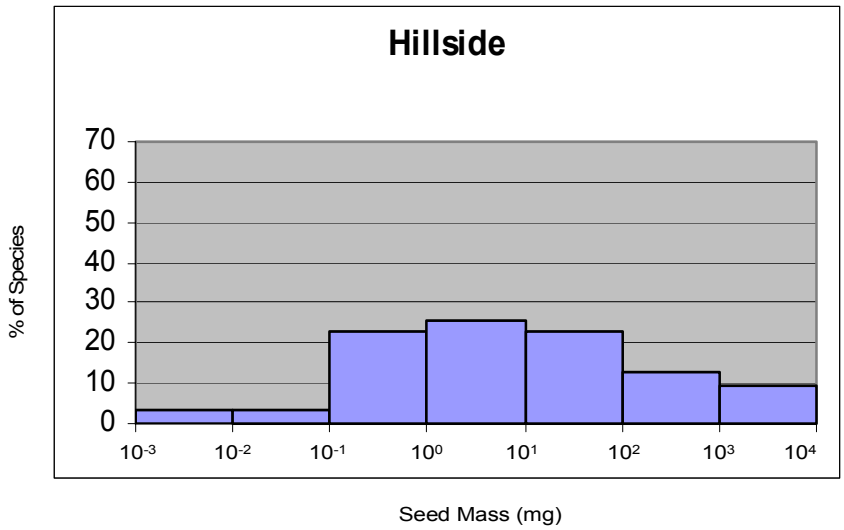
SAMPLE J1	MEAN (g):	2σ (g):	% OF TOTAL FRACTIONS:	CUMULATIVE %:
beaker B + ≤ -1.0Φ:				
≤ -1.0Φ:			0.00	0.00
empty beaker C:	79.82	0.01		
beaker C + 0.0Φ:	79.83	0.01		
0.0Φ:	0.01	0.02	0.05	0.05
empty beaker D:	85.46	0.01		
beaker D + 1.0Φ:	85.51	0.00		
1.0Φ:	0.05	0.01	0.40	0.45
empty beaker E:	154.29	0.00		
beaker E + 2.0Φ:	154.60	0.01		
2.0Φ:	0.31	0.01	2.58	3.03
empty beaker F:	181.27	0.01		
beaker F + 3.0Φ:	182.04	0.01		
3.0Φ:	0.77	0.01	6.37	9.40
empty beaker G:	192.78	0.01		
beaker G + 4.0Φ:	194.23	0.00		
4.0Φ:	1.45	0.01	11.98	21.37
empty beaker H:	408.58	0.00		
beaker H + >4.0Φ:	418.09	0.01		
>4.0Φ:	9.51	0.01	78.63	100.00
total fractions:	12.09		100.00	

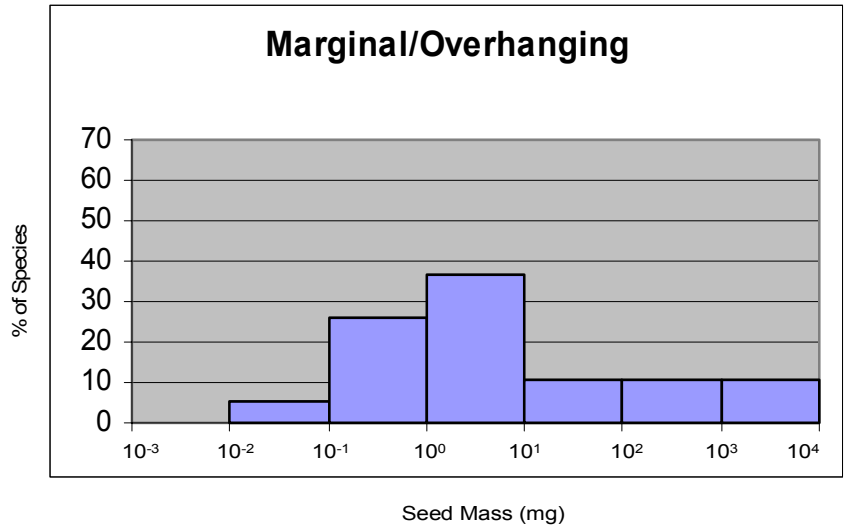
APPENDIX 3

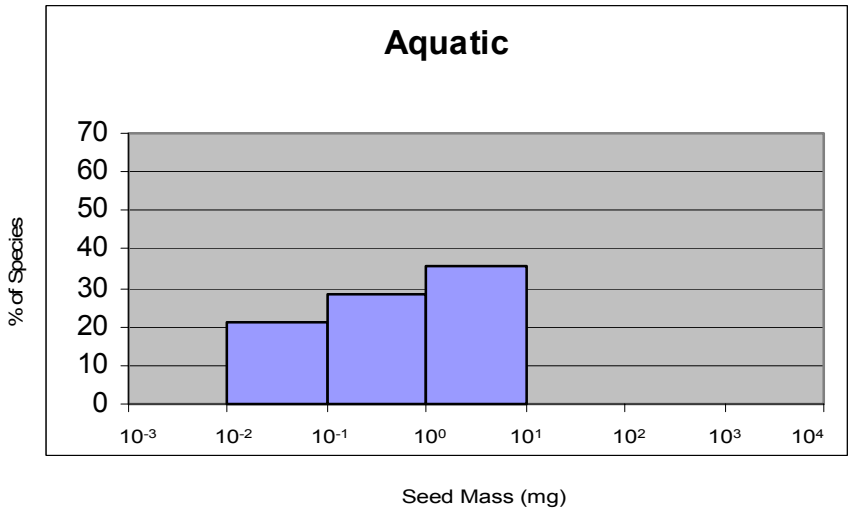
Histograms of Seed Size Distributions

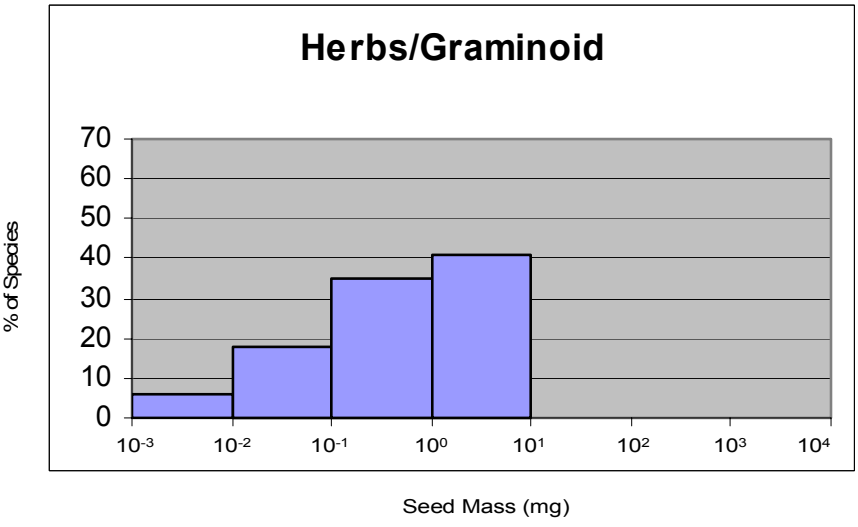
Histograms of the seed size distributions of the life and death assemblages, and subsets thereof, are presented here. "Entire Site" is the pooled data from the life assemblage. Different sections, growth forms, and dispersal modes within the life assemblage follow. "All Cores" is the pooled data from all 20 samples. Each sample is then presented individually.

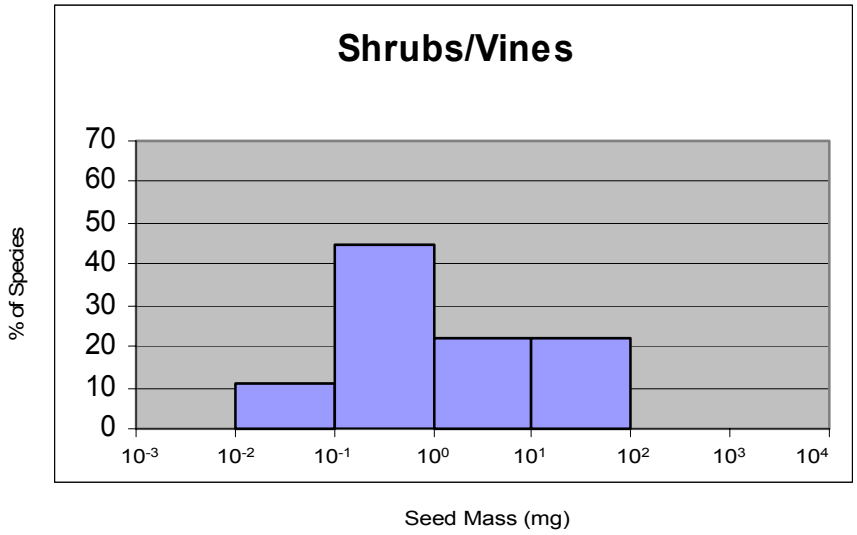


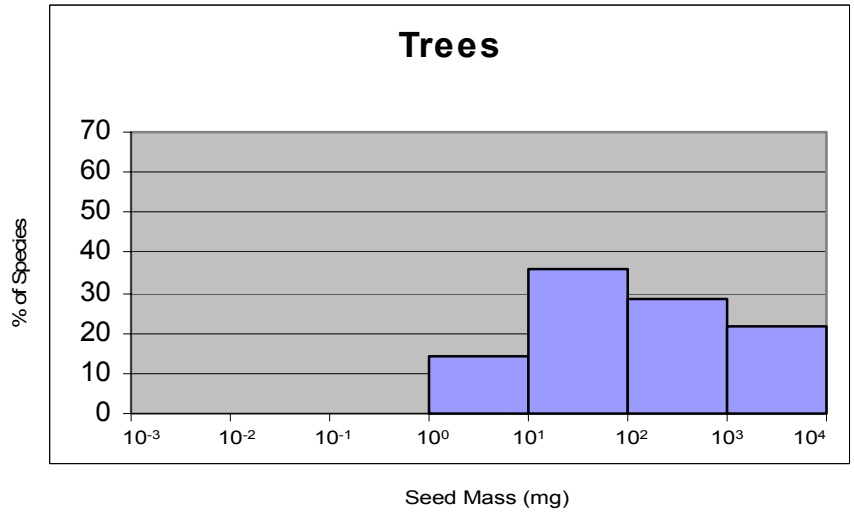


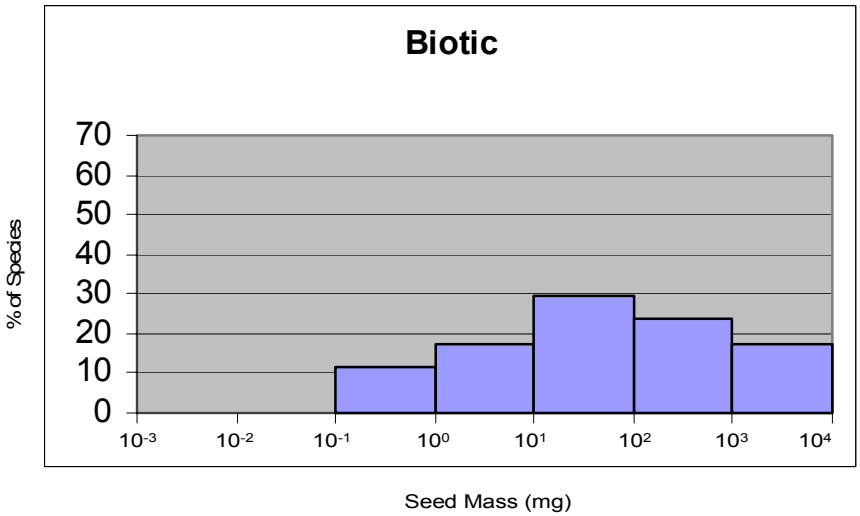

Marginal/Overhanging
% of Species
70
60
50
40
30
20
10
0
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

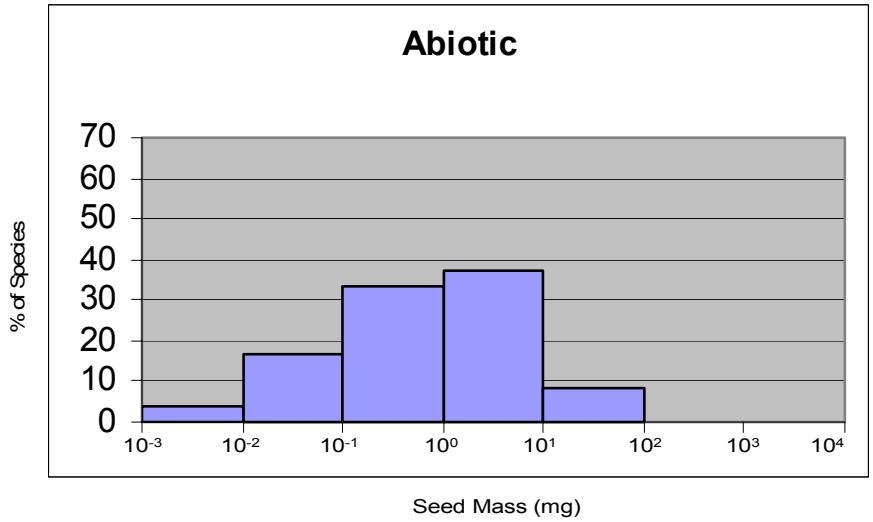

Aquatic
% of Species
70
60
50
40
30
20
10
0
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

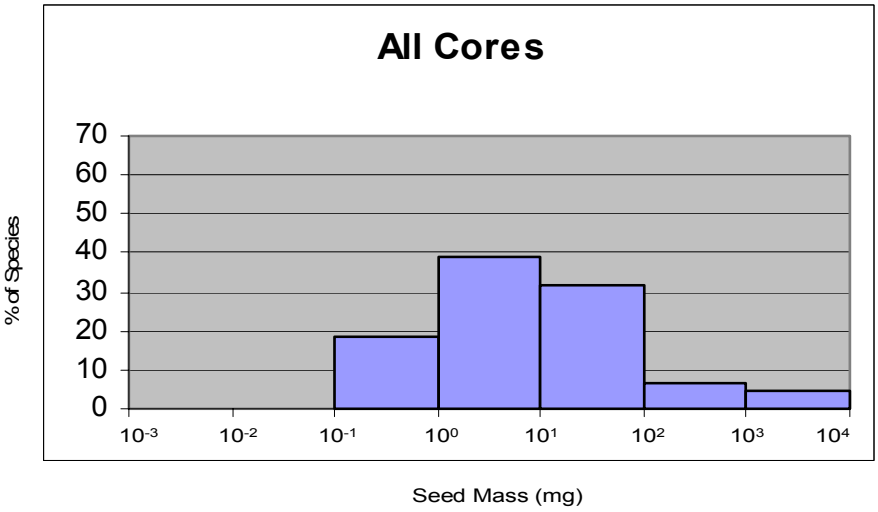

Herbs/Graminoid
% of Species
70
60
50
40
30
20
10
0
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

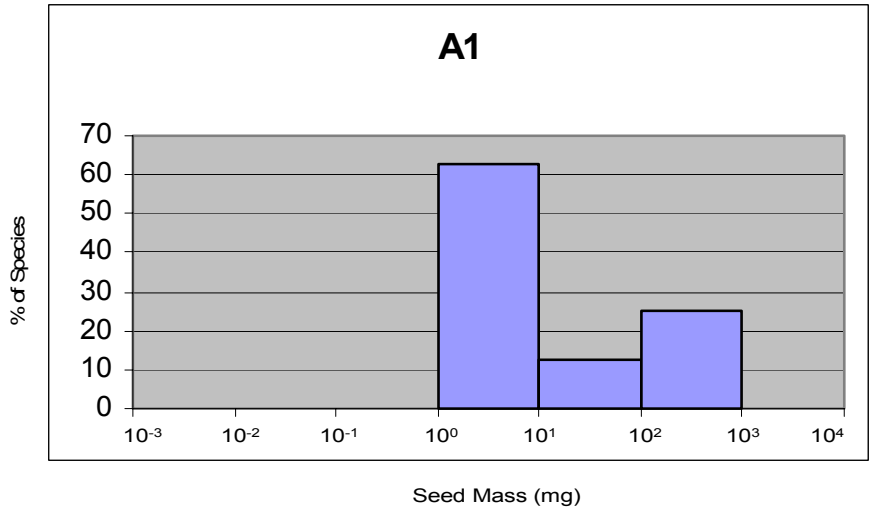

Shrubs/Vines
% of Species
70
60
50
40
30
20
10
0
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

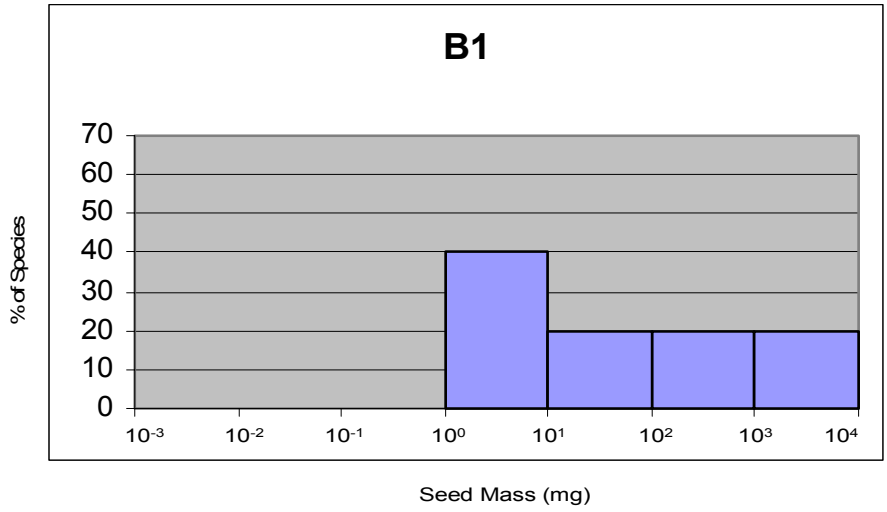

Trees
% of Species
70
60
50
40
30
20
10
0
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

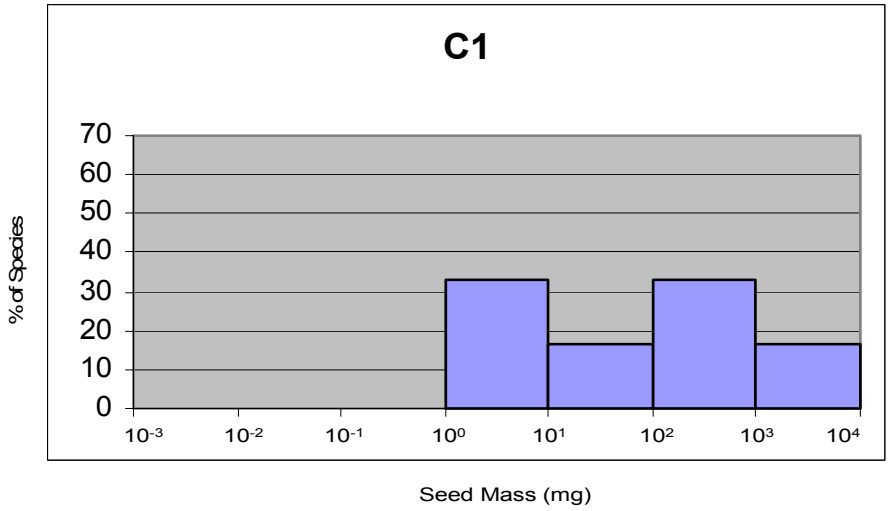

Biotic
% of Species
70
60
50
40
30
20
10
0
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

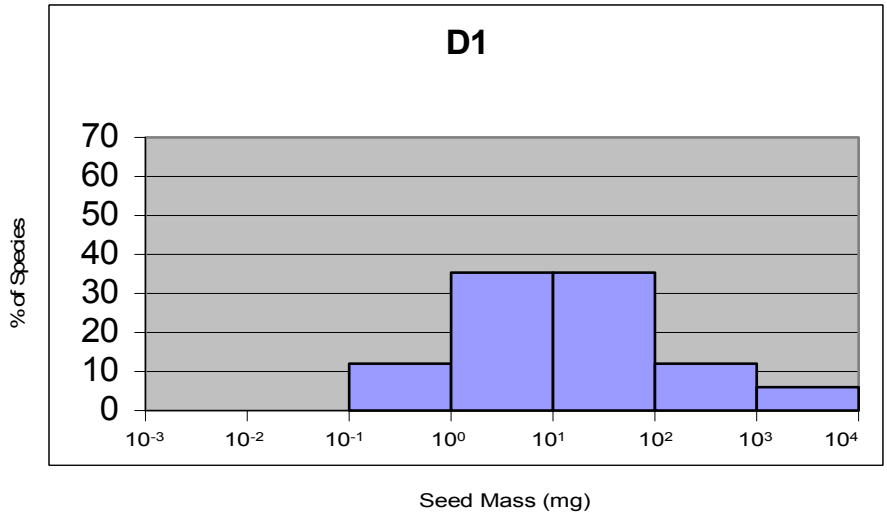

Abiotic
% of Species
70
60
50
40
30
20
10
0
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

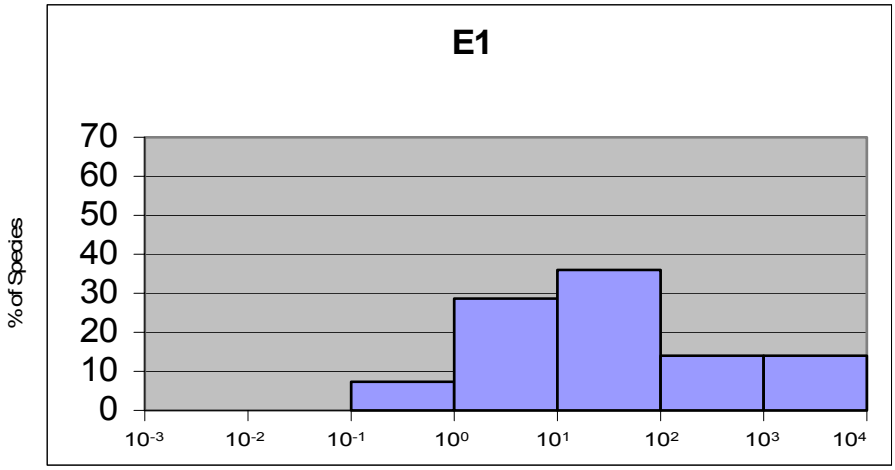

All Cores
% of Species
70
60
50
40
30
20
10
0
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

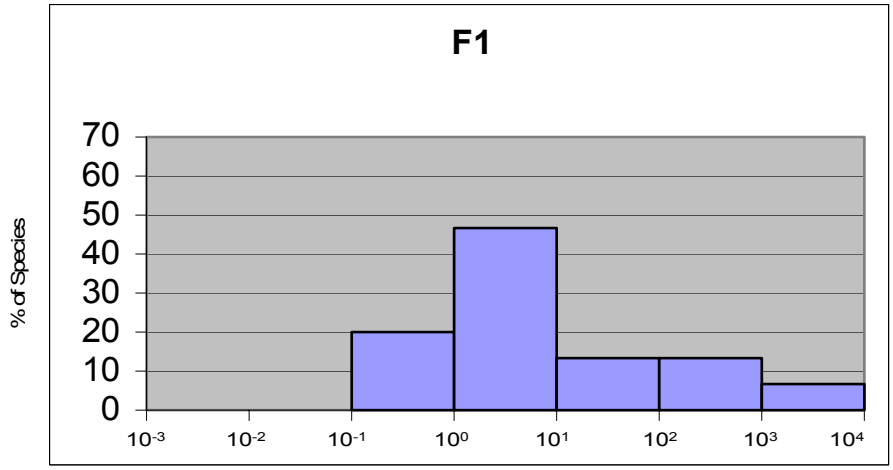

A1
% of Species
70
60
50
40
30
20
10
0
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

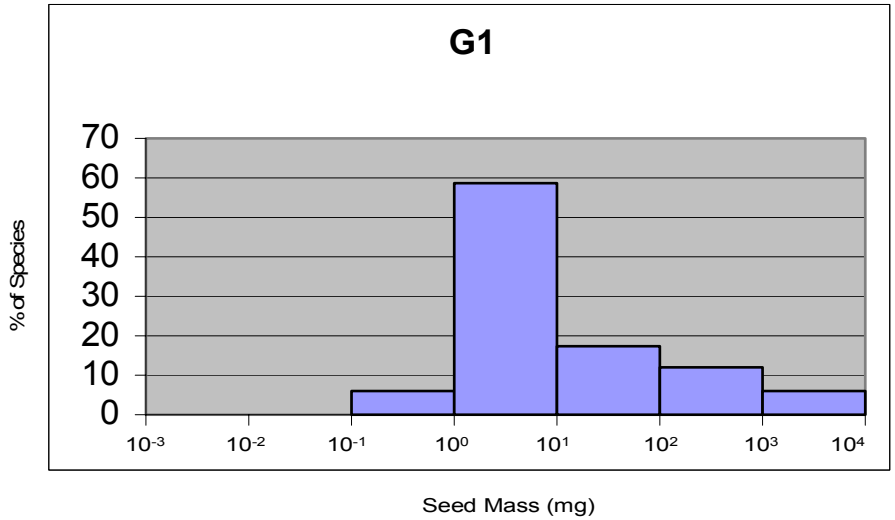

B1
% of Species
70
60
50
40
30
20
10
0
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

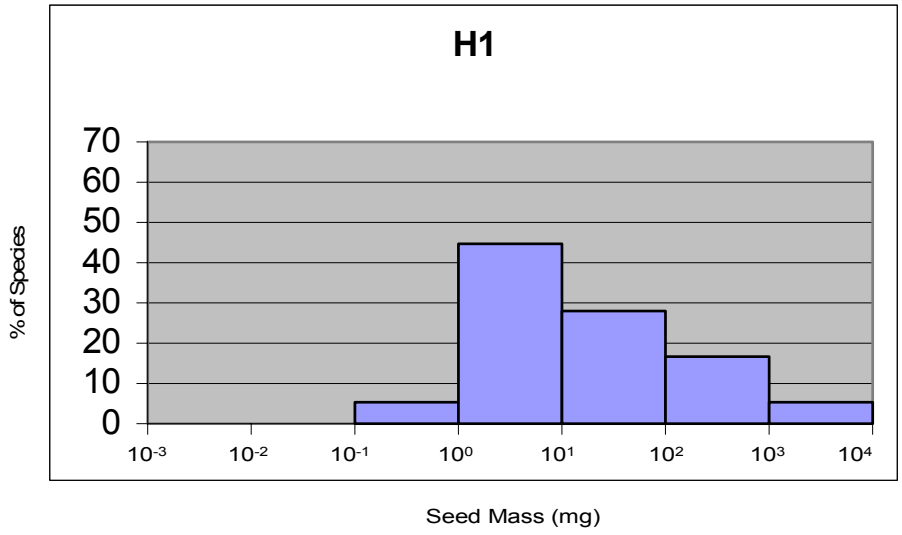

C1
% of Species
70
60
50
40
30
20
10
0
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

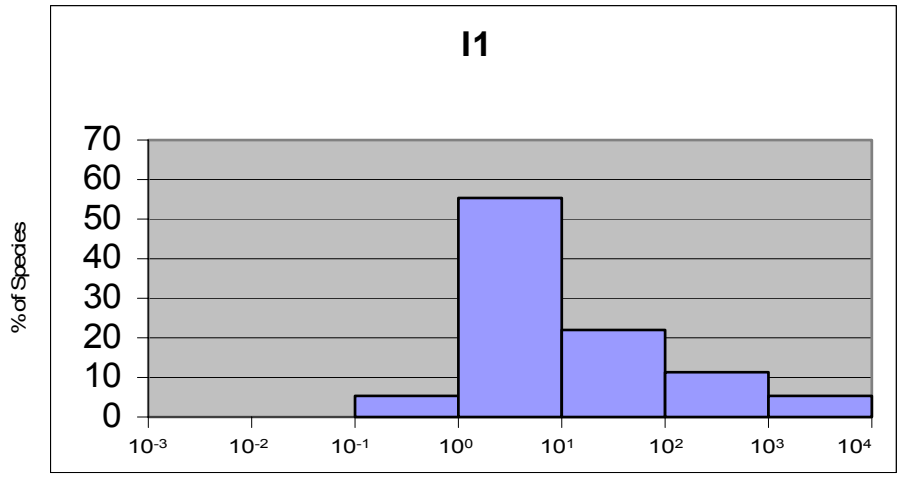

D1
% of Species
70
60
50
40
30
20
10
0
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

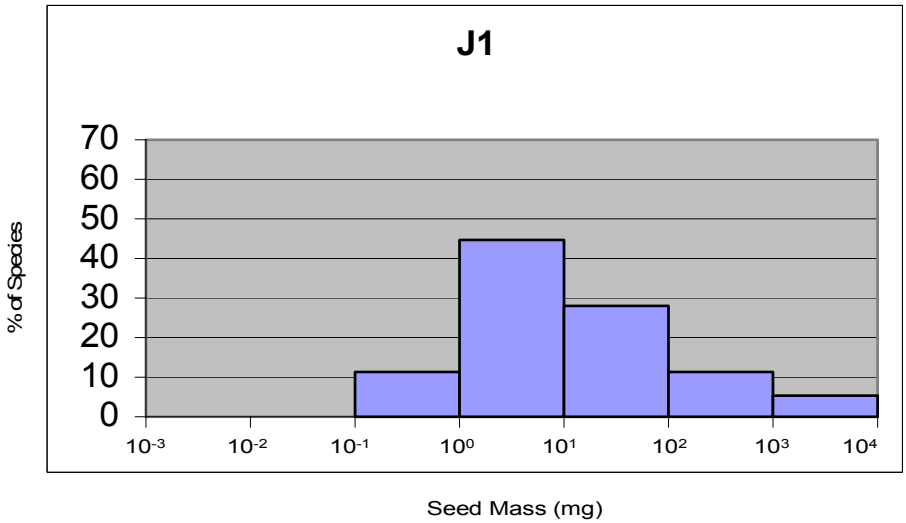

E1
% of Species
70
60
50
40
30
20
10
0
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

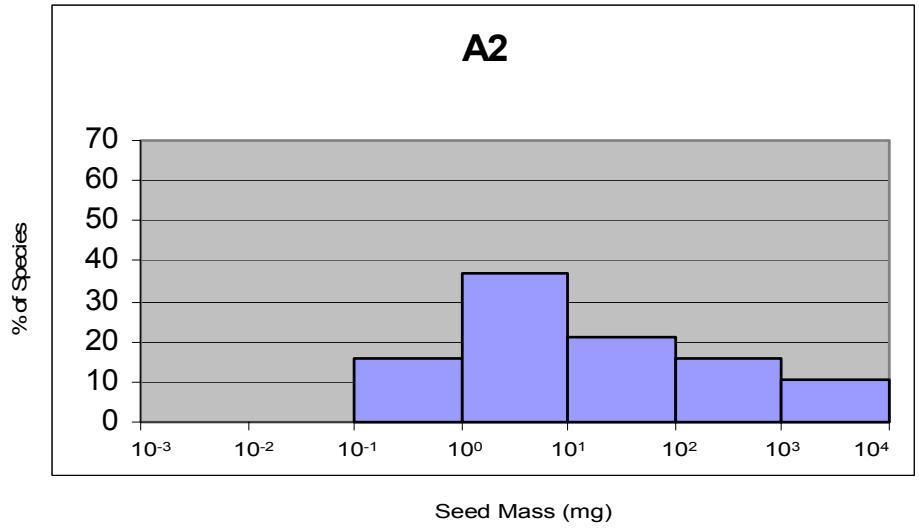

F1
% of Species
70
60
50
40
30
20
10
0
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

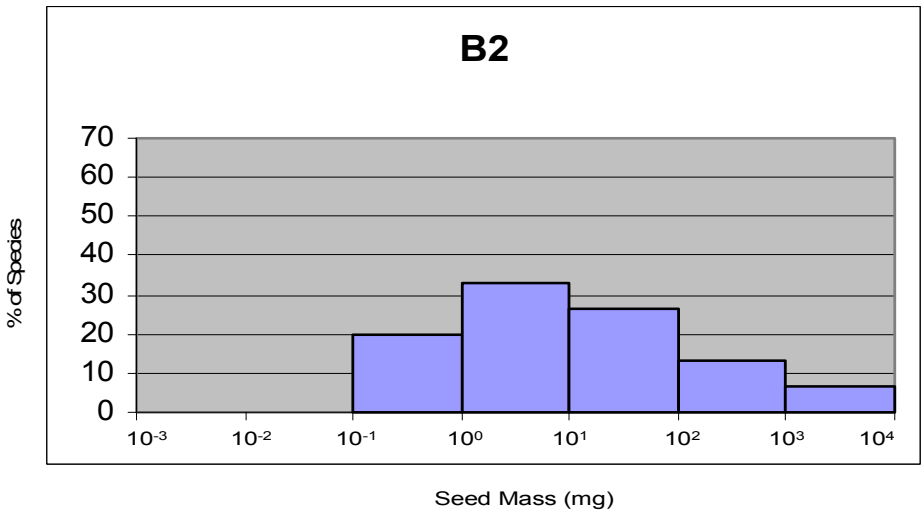

G1
% of Species
70
60
50
40
30
20
10
0
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

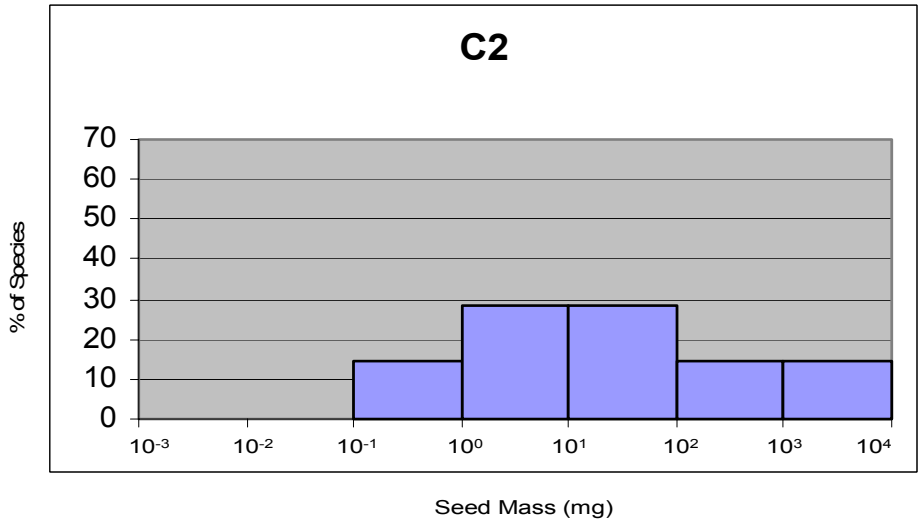

H1
70
60
50
40
30
20
10
0
% of Species
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

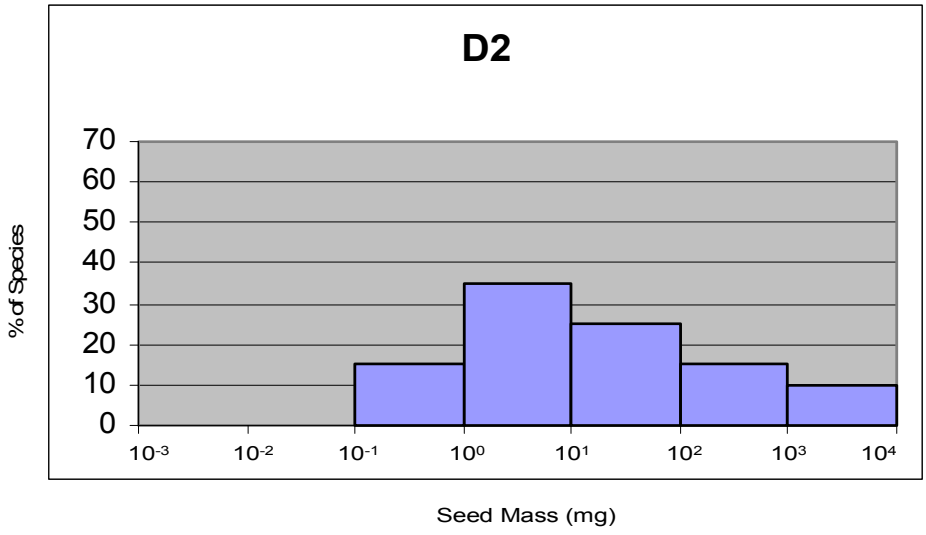

I1
70
60
50
40
30
20
10
0
% of Species
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

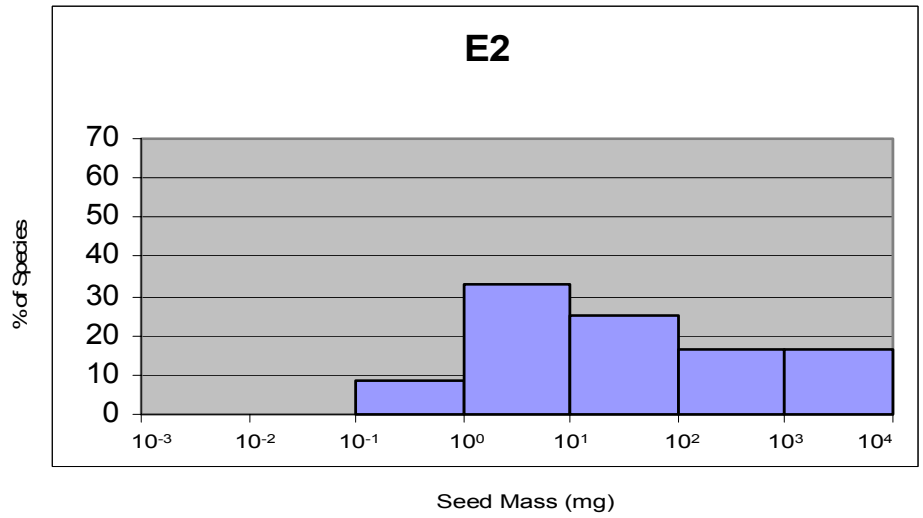

J1
70
60
50
40
30
20
10
0
% of Species
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

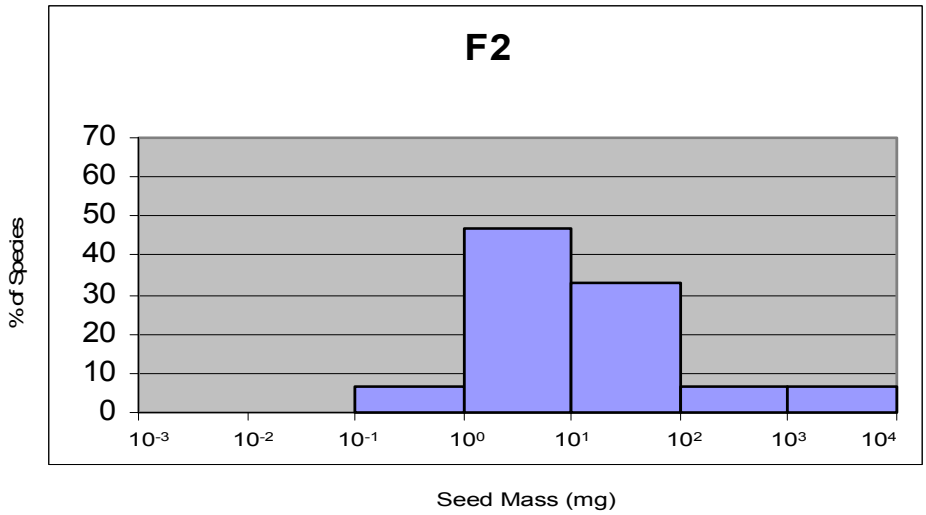

A2
70
60
50
40
30
20
10
0
% of Species
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

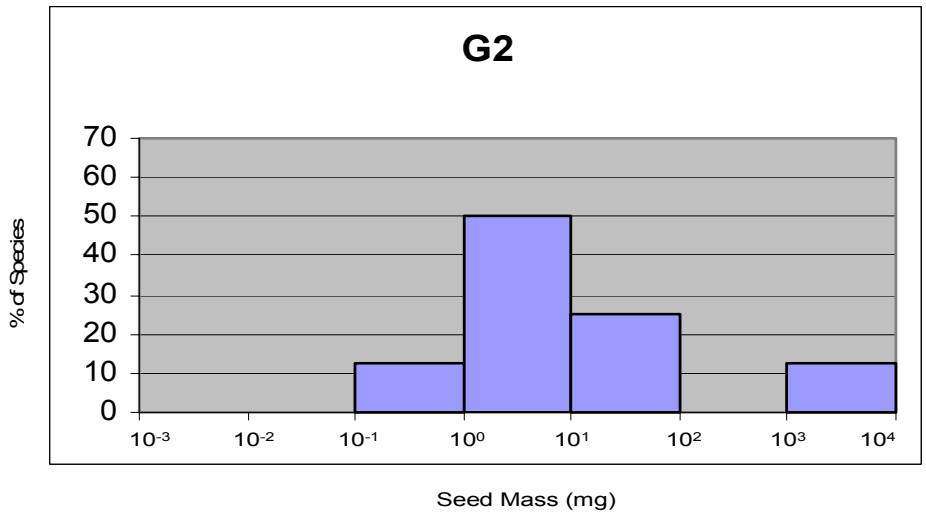

B2
70
60
50
40
30
20
10
0
% of Species
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

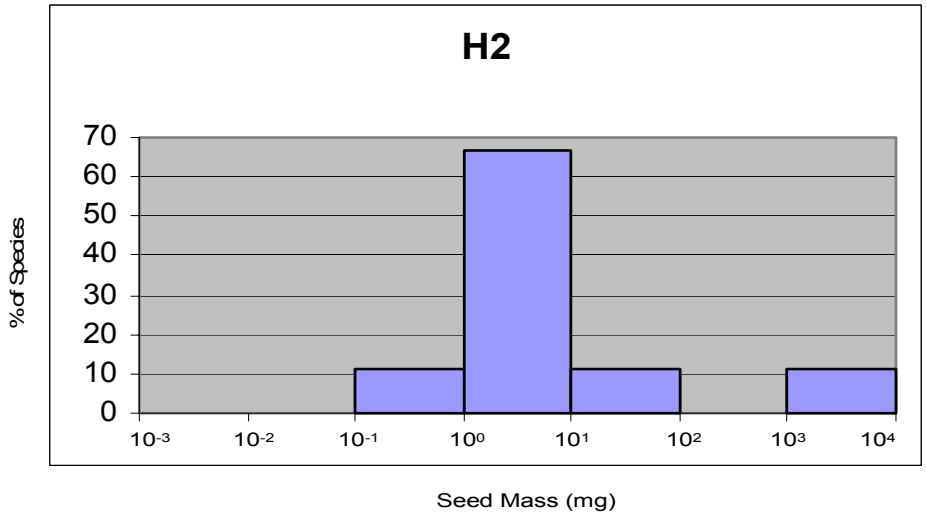

C2
70
60
50
40
30
20
10
0
% of Species
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

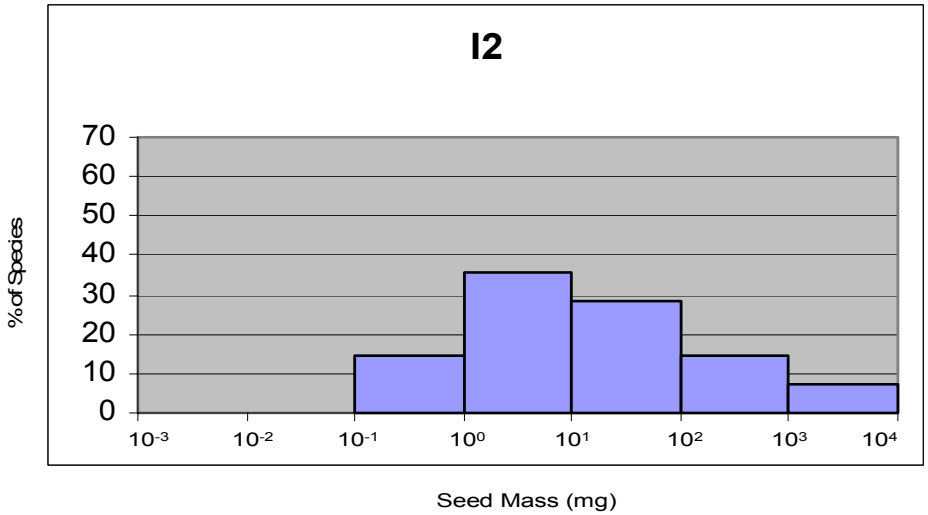

D2
70
60
50
40
30
20
10
0
% of Species
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)

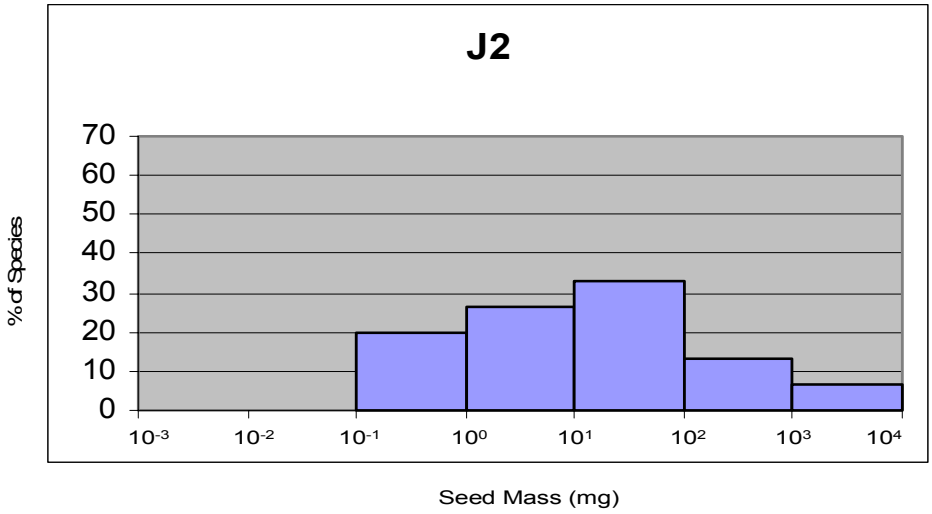

E2
70
60
50
40
30
20
10
0
% of Species
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)


F2
70
60
50
40
30
20
10
0
% of Species
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)


G2
70
60
50
40
30
20
10
0
% of Species
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)


H2
70
60
50
40
30
20
10
0
% of Species
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)


I2
70
60
50
40
30
20
10
0
% of Species
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)


J2
70
60
50
40
30
20
10
0
% of Species
10-3
10-2
10-1
100
101
102
103
104
Seed Mass (mg)